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MINIMUM INTENSITIES OF ILLUMINATION UNDER WHICH OWLS CAN FIND DEAD PREY BY SIGHT

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INTRODUCTION

IT is well known that owls are able to find their way about and to secure prey at night in very weak light. Few previous attempts, however, seem to have been made to determine the precise lower limit of an owl's vision.

In the experiments here reported an effort has been made to determine the weakest amount of illumination in which individuals of four species of owls are able to find the carcasses of freshly killed deer-mice (*Peromyscus maniculatus*). All the species of owls tested are known to feed in nature on Peromyscus and all of our captive owls fed readily on either live or dead mice belonging to this species.

The laborious daily work of conducting the experiments was performed by E. C. Sensenig, W. E. Howard, Elizabeth Barto, Mary Jane Lagler, and more briefly, by several other persons.

METHODS

The reaction room in which the experiments were performed is located in the Vertebrate Biology Building of the University of Michigan. It measures approximately nine by twenty-one feet in inside dimensions. There is a single door near one end of the room. A partition twenty-four inches high extends across the middle of the

room and divides it into two compartments, each nine by ten and one-half feet in size. The corners of each compartment are rounded by means of sheet-metal shields. Ventilation for the room is provided by an electric fan. There are light traps for the incoming and for the outgoing air. Special care has been taken to make the reaction room light-tight, but in spite of all precautions there is a slight amount of light leakage into the room, especially around the blocked-off windows and around the door. However, the amount of entering light is very slight, and one fails to see any trace of light until he has been in the darkened room for a number of minutes.

A perch for the owl extends across the room directly above the middle partition. It is about six feet above the floor. At one end of this perch is a large box to which the owl retires when the mice are being placed in position. The box has a door that swings open when its catch is released by pulling a string which extends outside the reaction room.

Illumination for the reaction room is provided by electric-light bulbs held in fixtures mounted on the ceiling over the middle of each of the two compartments. The lights are controlled from a panel outside the room. The controls include a rheostat and a time clock. The lamp fixture used for obtaining the weaker light intensities consists of a half-gallon tin can which completely surrounds a light bulb and which has an opening only on the lower end. The effective opening is $3\frac{1}{2}$ inches in diameter and is covered by a variable number of round sheets of paper. By increasing the number of sheets of paper the intensity of the illumination produced by the lamp may be reduced. The same type and thickness of paper, No. 3 University linen, was used in all the experiments. As many as sixteen sheets of this paper were used to reduce the illumination to the lowest intensities employed. The Mazda lamp bulbs used in this fixture were of two types: 10-watt daylight and 6-watt inside blue. When the resistance provided by the rheostat was introduced into the circuit the

light produced by either of these bulbs was reduced to approximately one-third its normal value. Surrounding this special fixture was a cluster of three light sockets, each with a large white enameled reflector. In these sockets there were used 50-watt daylight Mazda, 150-watt daylight Mazda, and No. 2 photoflood bulbs, as desired.

The hue of the light at the various intensities employed was not exactly the same. The light produced by the 6-watt inside-blue bulb is slightly more violet to our eyes than that produced by the 10-watt daylight bulb. An increase in the number of sheets of paper placed under the lamp bulb causes an apparently slight increase in blue tone. On the other hand, the reduction of light intensity by use of the rheostat makes the light appear less blue. No simple way of measuring these variations in hue has been found. It is believed, however, that the range of these variations in color is not very great. The over-all hue produced by the lamps appears to our eyes to be not very different at the several intensities used, being slightly more blue than daylight. The photoflood bulbs gave light somewhat richer in yellow and red than daylight, but these bulbs were used very little.

The measurement of the light intensities falling on the floor of the reaction room has been made by a special Weston illumination meter, model 603. The instrument is provided with two light-sensitive cells and measures the range from 0.02 to 2.00 foot-candles. This meter is able to measure directly only a small part of the range of intensities used in these studies. The values of the lower intensities were calculated by a proportional method. One of the cells of the photometer was covered and the other placed a few inches below the paper-covered opening of the ceiling lamp. The reading of the photometer could then be translated into light intensities falling on the floor by computation, using the rule that the decrease of light is proportional to the square of the distance. The proportional difference in light intensity produced by the several types of electric-light bulbs employed was also

determined, as was the effect on the light intensity of inserting the rheostat resistance. The reduction of light produced by additional sheets of paper in the lamp fixture was also measured, using the stronger bulb. By a series of calculations it was then possible to compute roughly the light intensity at the very dim illuminations.

No claim is made that the light intensities at the very weak illuminations used has been determined accurately. Numerous sources of error are involved in the calculations. The original readings of the photometer were of necessity rather rough, and any errors made at that time were of course multiplied in calculating the lower light intensities. The photometer, although calibrated for artificial light, was not accurately adjusted to the spectrum given by each of the several lamp bulbs employed. This would especially be true when the rheostat had reduced the bulb temperature and when the light had passed through a number of sheets of white paper in the lamp fixture. It is known, furthermore, that the voltage of the power line supplying the lamps was subject to considerable fluctuation. The intensity of light produced by each bulb undoubtedly varied also with its age. Although the amount of light leakage into the room was small it probably contributed an appreciable amount to the general illumination at the lower light intensities employed. The slight amount of diffuse light reflected from the walls and floor of the reaction room also could not be estimated. The calculations of light intensity should therefore be considered to be only rough approximations.

The procedure of each experiment was to cover the floor of one compartment in the reaction room with soil of a light color, the other compartment with a soil of a dark color. Two colors of mice were also employed, one type roughly matching the color of the lighter soil, the other that of the darker soil. One mouse of each color was killed and then, while the owl was in his box, the bodies of the two mice were placed in a more or less natural position on the floor, both usually in the same

compartment. The positions of the mice on the floor of the compartment were usually changed for each experiment, so that the owl could not form the habit of searching in a particular place. In general, the mice were placed alternately on successive days in each of the two compartments. After the bodies of the mice were in position the door of the reaction room was closed, the illumination of the room adjusted to the proper intensity, and the owl released by pulling the string that opened the door of his box.

The owl was then allowed to search for the mice overnight or for a given interval of time, after which he was made to retire to his box and the mice which remained were counted. A mouse found by the owl and either eaten or moved by him to a new position was counted as a capture, whether or not the mouse was eaten immediately.

After the experiments for the day were completed the owl was given additional mice for food, but these were removed after they had been exposed for a few hours, so that at the time for beginning the experiment on the following day the owl was always hungry.

In the attempt to keep the conditions as natural as possible for the owl the reaction room was left dark about twelve hours of each twenty-four and was illuminated by six 150-watt Mazda daylight bulbs during the other twelve hours. These lights were controlled by a time clock. The periods of light and dark were, in some of the experiments, purposely set out of step with the dark and light periods of normal night and day, so that the time each day when the experiments were begun would approximate in diurnal time the coming of darkness and the beginning of usual owl activity.

The soils used in the experiments were of two types, here called, respectively, silica sand and gulley soil. The silica sand, which is a regular article of commerce, i whitish in color. The gulley soil was secured from a small eroded gulley in some filled-in land alongside the

laboratory building. This soil evidently contained very little humus. It was a dull, slightly yellowish gray in color.

The dead mice employed were of three types: albino, ivory, and gray. All of them were laboratory strains of the deer-mouse (*Peromyscus maniculatus*). The ivory mice were a close match in color with the silica sand. The albino mice were more nearly white than the silica sand and therefore they contrasted with it slightly in shade. The gray mice were a mixed lot of animals discarded from time to time from the laboratory stock. A few of them matched the gulley soil fairly well in color, but some were different from this soil in hue and many of the were considerably darker in shade.

Results of the Experiments

The experiments here described were seriously begun in the fall of 1938, when the special reaction room above described was constructed for the purpose. Tentative experiments had been initiated a number of years earlier, but had to be given up because of the lack of a satisfactory place for the study. All the experiments here reported were completed before the end of 1943.

Barred Owl

The barred owl (*Strix varia*) used in these studies was an adult female presented by Hugh S. Davis, who secured it at Tulsa, Oklahoma. Its subspecies has not been determined.

In fairly bright light the barred owl has no difficulty in seeing mice at a distance of ten feet or more. Several times while we were watching her the owl pounced from her perch onto live mice which were running about on the floor of the room. Her method was to drop on the floor near the mouse, throw her wings more or less around the animal, and seize it in one of her talons. The maneuver was carried out very rapidly and it was difficult to observe the precise details. At light intensities of 8.5, 0.4, and 0.3

foot-candles the owl evidently distinguished the mouse clearly and attacked it directly. These intensities correspond, respectively, to weak daylight and to the light given by the full moon overhead on a very clear night. There is nothing to indicate that this owl would not be able to see well in still brighter light.

In dim lights the movements of the owl could not be clearly seen by the human observer. By noting the tracks of the owl in the sand on the floor of the reaction room, however, an indication was secured whether the owl was able to pounce directly upon or near a dead mouse or whether she approached it by stalking. With light from a 6-watt inside-blue bulb, reduced by the rheostat, and passed through nine sheets of paper (producing about 0.000,000,73 foot-candle of illumination on the floor) the owl was able to pounce directly upon or near a dead mouse, and did so repeatedly, as shown by her tracks at the position where the mouse was placed.

When the light was dimmed by ten sheets of paper (giving about 0.000,000,53 foot-candle of illumination) the owl was still sometimes able to drop directly onto the position of a dead mouse. Out of ten mice exposed during five nights on silica sand at this light intensity two albino mice were pounced upon directly, four albino and two gray mice were secured by extensive searching on foot, and two albino mice were not found by the owl.

With eleven sheets of paper (0.000,000,35 foot-candle) and at still weaker light intensities, with one exception, the owl was never able to pounce directly onto the dead mouse, but always approached it on foot. In the one exception noted the tracks in the sand indicated that the owl had dropped directly onto a dead mouse in complete darkness. On this occasion, however, a dead mouse had been placed in exactly the same position for several successive nights and it seems probable therefore that the owl had developed a position habit. In subsequent trials the positions of the dead mice were changed each night, and the owl then was not able to secure any mice in the dark.

At some of the lower light intensities employed the barred owl evidently was able to see the mouse when she was close to it, though she could not pounce directly upon it from a distance. Often her tracks in the sand seemed to be aimless until she came within a foot or so of a mouse, whereupon she went directly to it. This type of behavior was particularly noticeable when eleven or twelve sheets of paper were used to reduce the light to calculated intensities of 0.000,000,35 or 0.000,000,25 foot-candle, respectively. With eleven sheets of paper, however, the owl on one occasion passed within six inches of a mouse without finding it.

At the lowest light intensities employed and in darkness the barred owl usually was unable to find the dead mice, even though she was allowed to search for the whole night. In the morning the floor of the reaction room would show many tracks, especially in the vicinity of places where mice had been secured on previous nights.

In order to exhibit more precisely the lower limit of illumination at which the barred owl could find the dead mice the most extensive series of experiments performed is summarized in Table I. In these experiments two dead mice were exposed to the owl each night.

It will be noted from the table that the owl was able to secure mice at somewhat lower light intensities on the nearly white silica sand than on the darker-colored gulley soil. Thus, the owl secured no mice on the gulley soil under illuminations below 0.000,000,19 foot-candle, but she secured five mice out of eight exposed on silica sand at an illumination of 0.000,000,15 foot-candle. The reflection of light from the pale-colored silica sand evidently slightly increased the effective light intensity in that compartment.

Also, it will be noted that mice contrasting in color with the background on which they were placed were taken at somewhat lower light intensities than those that were of a color more nearly matching that of the soil. No albino mice were taken on silica sand under an illumination of

TABLE I

BARRED OWL. NUMBER OF DEAD DEER-MICE FOUND IN LIGHT OF VARIOUS INTENSITIES AND IN DARKNESS. TWO MICE EXPOSED TO ONE OWL OVERNIGHT IN EACH TRIAL

Illumination in foot-candles	Silica sand				Gulley soil				Mice taken per night Average
	Albino mice		Gray mice		Albino mice		Gray mice		
	Number exposed	Per cent. taken	Number exposed	Per cent. taken	Number exposed	Per cent. taken	Number exposed	Per cent. taken	
0.000,001,05	..	..	..	...	1	100	5	80	1.7
0.000,000,73	1	0	1	100	2	100	6	67	1.4
0.000,000,53	3	67	7	100	5	60	5	20	1.3
0.000,000,35	3	67	7	100	4	100	6	17	1.4
0.000,000,25	4	50	4	100	3	100	5	20	1.3
0.000,000,19	8	25	15	67	4	50	9	0	.8
0.000,000,15	3	0	5	100	5	0	3	0	.6
0.000,000,11	1	0	5	20	..	...	..	..	.3
0.000,000,08	..	..	6	0	..	...	..	..	.0
Dark	..	..	10	10	..	...	..	..	.1

less than 0.000,000,19 foot-candle, but gray mice were secured on this color of soil under light intensities of both 0.000,000,15 and 0.000,000,11 foot-candle. Likewise, on the gulley soil no gray mice were taken at an illumination less than 0.000,000,25 foot-candle, but several albino mice were secured by the owl at an illumination of only 0.000,000,19 foot-candle. These data are in harmony with the general observation that objects contrasting in color with their background are more easily perceived than those that harmonize with it.

It is evident then that in stating the minimum light intensity at which an owl can see its prey the color of the soil and of the prey must both be specified.

An inspection of the table will reveal that for any given color of mouse and of soil there is no exact light intensity at which the owl suddenly fails to find prey. On the contrary, there is in general a gradual dropping off in the percentage of prey secured as the illumination becomes dimmer. It is not easy to determine the precise lower limit of vision of the owl, because she secured an occasional mouse in extremely dim light and in darkness, obviously by searching on the floor of the room until she came into contact with a carcass.

The barred owl seemed to have no great difficulty in finding gray-colored mice on silica-sand soil at a light intensity calculated to be 0.000,000,15 foot-candle. These are the most favorable conditions for vision. At this very dim illumination she was not able to find albino mice on silica-sand soil, nor any mice at all on the darker-colored gulley soil. At an illumination of 0.000,000,11 foot-candle the owl secured only one mouse in five trials, this one probably by chance.

The failure of the owl to secure all the mice exposed at the higher light intensities does not demonstrate any lack of vision at those illuminations. Often the owl secured one mouse during the night and did not search any more, perhaps because she was no longer hungry.

These experiments demonstrate that the barred owl

is able to see in extremely dim light. At a light intensity calculated to be 0.000,000,73 foot-candle the bird certainly was able to see mouse carcasses of various colors on silica-sand soil at a distance of six feet or more. This is proved by her ability to pounce from her perch directly onto the mice. At a light intensity calculated to be 0.000,000,53 foot-candle she was only occasionally able to pounce directly onto a carcass, but found her prey by searching on foot. It seems almost certain that she is able to see a mouse carcass in light of this intensity when she is within a foot or less of it. By searching on the floor of the reaction room the owl was able to find dark-colored mice with considerable frequency on nearly white soil in light intensities calculated to be as low as 0.000,000,15 foot-candle. In such dim light the owl never found the mouse carcasses that were not contrasting in color with the soil nor did she find any carcasses on dark-colored soil. There is no evidence from these experiments that this particular barred owl was able to see anything at all in light intensities below 0.000,000,15 foot-candle.

Long-eared Owl

The long-eared owl (*Asio wilsonianus*) used in these experiments was captured in Pennsylvania and was kindly presented to us by the Pennsylvania Game Commission through Dr. Richard Gerstell. The bird was evidently adult when received by us. It is still alive and its sex has not been determined.

This long-eared owl regularly captured living and dead deer-mice exposed in light of moderate to strong intensities. A series of experiments designed to determine the lowest limit of light intensity in which the owl could secure Peromyscus carcasses is summarized in Table II. In these experiments one dead deer-mouse of ivory color and one of gray color was exposed to the owl each night.

In light passed through eight sheets of paper (0.000,001,05 foot-candle calculated) the owl made few tracks in the sand on the floor of the reaction room and seemed

TABLE II

LONG-EARED OWL. NUMBER OF DEAD DEER-MICE FOUND IN LIGHT OF VARIOUS INTENSITIES AND IN DARKNESS. TWO MICE EXPOSED TO ONE OWL OVERNIGHT IN EACH TRIAL

Illumination in foot-candles	Silica sand				Gulley soil				Mice taken per night Average
	Ivory mice		Gray mice		Ivory mice		Gray mice		
	Number exposed	Per cent. taken	Number exposed	Per cent. taken	Number exposed	Per cent. taken	Number exposed	Per cent. taken	
0.000,001.05	8	75	8	75	8	88	8	88	1.63
0.000,000.25	8	25	8	88	8	100	8	13	1.13
0.000,000.08	8	25	8	38	8	38	8	13	.56
Dark	8	0	8	0	8	25	8	25	.25

to have no difficulty in locating the mice directly from his perch. When twelve sheets of paper were used, reducing the light intensity to 0.000,000,25 foot-candle, the owl evidently was not able to see well at a distance and he made many tracks in the sand in searching for the dead mice. In one trial at this light intensity, the owl actually walked over a gray-colored mouse lying on gulley soil and moved the carcass slightly in position without securing it. At still weaker light intensities the owl made many tracks on the floor of the reaction room. He secured a few mouse carcasses, however, even in complete darkness. It may be doubted that the owl was able to see anything at all in the slight amount of light passed through sixteen sheets of paper (0.000,000,08 foot-candle), and it is believed that the mouse carcasses secured at this light intensity and in complete darkness were secured only by the owl accidentally coming into contact with them in his meanderings on the floor of the reaction room.

These data fail to prove any greater ability of this owl to secure mouse carcasses of one color or on one color of soil than another at any light intensity. However, the number of records secured at the lower light intensities is few.

So far as may be told from these rather meager experiments the long-eared owl is able to see from a distance of six feet or more and to pounce directly upon prey when the light intensity is 0.000,001,05 foot-candle. The lower limit of illumination at which the long-eared owl is able to see dead prey close at hand is indicated to lie between 0.000,000,25 and 0.000,000,08 foot-candle.

Barn Owl

The barn owl (*Tyto alba pratincola*) used in these experiments was presented by John Craighead, who had captured it in southern Michigan. It is still alive and its sex is unknown.

In most of the experiments with the barn owl the bird was allowed only a 20-minute period in which to secure

his prey, instead of a whole night (Table III). These experiments were performed in the morning after the owl had been exposed to light of approximately nine foot-candles intensity for the preceding night, in the attempt to make him reverse his usual diurnal cycle of activity. If the owl failed to secure a mouse in the first 20-minute trial period of the day, he was given additional test periods, each counting as a trial. Each successive trial was, however, carried out at a light intensity somewhat different, usually stronger, than the preceding one. The owl thus was sometimes given two or three, or very rarely four, trials in one morning.

Under an illumination calculated to have been 0.000,002 foot-candle the barn owl secured six mice in ten trial periods and it seems evident that he could see very well in this amount of illumination. At a light intensity estimated to be 0.000,000,53 foot-candle he secured one of the two dead mice placed in the room in three trials out of ten. In this dim light he, therefore, undoubtedly had some difficulty in seeing the mice. At a dimmer illumination estimated to be 0.000,000,31 foot-candle he secured only one mouse in ten trials. At a still weaker light intensity, estimated to be 0.000,000,08 foot-candle, the owl failed to secure any mice. Some of the mice taken in the weaker light intensities were undoubtedly located by the owl through random searching in the dark, but this could hardly account for his being successful in securing three mice in ten trials at the intensity of 0.000,000,53 foot-candle. In complete darkness the owl secured only one mouse in twenty trials.

It will be noted from the table that the barn owl failed to take any mice in ten trials under an illumination of 0.000,013 foot-candle. Also at several other light intensities he was successful only part of the time, although he later demonstrated his ability to secure mice in considerably weaker light. The explanation for these failures seems to be that this owl was very timid and that he had not become fully accustomed to his surroundings at the

TABLE III

BARN OWL. NUMBER OF DEAD DEER-MICE FOUND IN LIGHT OF VARIOUS INTENSITIES AND IN DARKNESS. TWO MICE EXPOSED TO ONE OWL FOR 20-MINUTE PERIODS

Illumination in foot-candles	Silica sand				Gulley soil				Mice taken per period Average
	Ivory mice		Gray mice		Ivory mice		Gray mice		
	Number exposed	Per cent. taken	Number exposed	Per cent. taken	Number exposed	Per cent. taken	Number exposed	Per cent. taken	
8.5	5	0	5	40	5	0	5	20	.6
1.58	5	40	5	40	5	20	5	50	1.5
.24	5	10	5	30	5	10	5	20	.7
.000,1	5	0	5	10	5	0	5	10	.2
.000,026	5	0	5	40	5	0	5	20	.6
.000,013	5	0	5	0	5	0	5	0	.0
.000,003,5	5	10	5	10	5	0	5	0	.0
.000,002	5	10	5	30	5	10	5	10	.6
.000,000,53	5	10	5	10	5	10	5	0	.3
.000,000,31	5	0	5	10	5	0	5	0	.1
.000,000,08	5	0	5	0	5	0	5	0	.0
Dark	10	0	10	0	10	0	10	10	.05

time when these early experiments were carried out. There seems to be no doubt that the barn owl can detect and secure mice over a great range of light intensities, for he demonstrated an ability to see in very weak illuminations as well as in fairly strong ones.

This owl exhibited, early in the tests, a decided preference for the gray over the ivory mice offered. Efforts to break him of this preference were not entirely successful, for the total number of gray mice (36) taken considerably exceeds that of the ivory mice (13).

In these experiments, as in those with the barred owl, there is a tendency under weak illumination for more mice to be secured on the nearly white silica sand than on the gray gulley soil. This difference is assumed to be due to the greater amount of light reflected from the lighter colored soil, which presumably increases the total illumination in that compartment to a slight extent.

In a few experiments the barn owl was given the whole night to search for mouse carcasses on the floor of the reaction room. In these experiments two dead gray mice were placed each night on silica sand, to which they contrasted conspicuously in shade of color. For five nights the light intensity was adjusted to an amount calculated to have been 0.000,000,08 foot-candle. Under this amount of illumination the barn owl secured both dead mice on each of three nights and one mouse on one night. On the other night the owl evidently did not leave his perch, for he secured no mice and there were no tracks in the sand. For five other nights, alternating with the first set, the reaction room was in complete darkness. Nevertheless, the owl secured both mice on two nights and one mouse on each of two other nights. On one night he secured no mouse, though he searched diligently, as shown by the numerous tracks he made in the sand.

Every morning, except two, during the period this later series of experiments was being conducted the sand on the floor of the reaction room was found to be covered by tracks of the owl. On one night, as above mentioned, no

tracks were made on the floor and the owl failed to secure a mouse. On the other exceptional night the owl secured one mouse in complete darkness, but there were tracks only within a foot or two of the place where the mouse was secured. In this instance the bird may possibly have found his prey shortly after his first descent to the floor and then did not search farther that night.

It seems evident, therefore, that under very weak illumination and in complete darkness the barn owl secured his prey mostly by walking about on the floor of the reaction room until he came into contact with a carcass.

The fact that the barn owl was somewhat more successful than the barred owl or long-eared owl in securing mice in very weak illuminations and in darkness during an over-night period seems to be due to his greater energy in searching. Although both of these other species of owls did search for the mice on the floor of the reaction room, as shown by their tracks in the sand, neither of them made as many tracks as did the barn owl.

These experiments demonstrate that under these laboratory conditions the barn owl undoubtedly is able to see dead mice six or more feet away under an illumination calculated to be 0.000,002 foot-candle, but that he has some difficulty in seeing the carcasses under the most favorable conditions when the incident light is reduced to 0.000,000,53 foot-candle. Under illuminations dimmer than this the owl probably secured his prey almost entirely by searching on the ground on foot.

Burrowing Owl

The western burrowing owls (*Speotyto cunicularia hypugaea*) used in this study consisted of two females from Alamogordo, New Mexico, secured from H. G. Clark. This owl is considerably more diurnal in habit than the other species used in this investigation. In their natural habitat, burrowing owls are frequently seen in early morning or late afternoon perched on fence posts or other points of vantage. It, therefore, is of considerable

interest to discover whether they are able to see their prey in such dim illuminations as the more nocturnal, forest-inhabiting kinds of owls.

Both burrowing owls ran about incessantly over the floor of the reaction room, much more so than did the other species of owls tested. It seems evident that much of their prey must be secured by being run down, rather than swooped upon. Every night the floor of the experimental room would be completely covered by the tracks of the two owls. This habit made difficult the exact determination of the lower limit of illumination under which the owls could see. It was impossible to be certain that a dead mouse taken during an experiment actually was located by sight rather than stumbled upon in the course of the meanderings of the owls. To make the finding of the mice more difficult for the owls they were given only a 20-minute period in which to secure their prey, instead of a whole night.

At the highest light intensities which were used in the experimental room (109 foot-candles) the owls were able to locate the mice satisfactorily and there was no indication that this amount of light was the least handicap to them. Together they secured an average of 1.3 mice in each of nine 20-minute periods (Table IV). From their habits it seems probable that they often feed in full sunlight.

In light intensities down to and including 0.000,026 foot-candle the owls secured an average of about one dead mouse on each 20-minute trial. At light intensities lower than this they were generally unsuccessful. At an intensity of 0.000,013 foot-candle the two owls together found only one mouse in ten trials, and at 0.000,003,5 foot-candle only two mice in ten trials. In complete darkness they were able to find one mouse in ten trials. It seems certain that the mice secured at the lower light intensities, like those found in darkness, were located by chance, rather than by sight.

When the owls were given the whole night to search for

TABLE IV

BURROWING OWL. NUMBER OF DEAD DEER-MICE FOUND IN LIGHT OF VARIOUS INTENSITIES AND IN DARKNESS. TWO MICE EXPOSED TO TWO OWLS FOR 20-MINUTE PERIODS

Illumination in foot candles	Silica Sand				Gulley Soil				Mice taken per period Average
	Ivory mice		Gray mice		Ivory mice		Gray mice		
	Number exposed	Per cent. taken	Number exposed	Per cent. taken	Number exposed	Per cent. taken	Number exposed	Per cent. taken	
109	4	50	4	0	5	60	5	40	1.3
8.5	5	20	5	40	5	80	5	0	.7
1.58	5	60	5	40	5	60	5	40	1.0
0.24	5	60	5	80	5	60	5	40	1.2
0.017	5	100	5	20	5	100	5	20	1.2
0.004,5	5	60	5	80	5	100	5	0	1.2
0.000,1	5	0	5	40	5	60	5	0	.5
0.000,026	5	40	5	60	5	80	5	20	1.0
0.000,013	5	0	5	20	5	0	5	0	.1
0.000,003,5	5	0	5	20	5	20	5	0	.2
Dark	6	17	6	0	5	0	5	0	.1

the dead mice they were more successful than in the 20-minute periods. At a light intensity calculated to be 0.000,001,05 foot-candle they secured six mice in ten nights. The owls, however, also found six mice in ten nights in complete darkness. It therefore seems certain that these mice must have been secured mostly by chance encounters rather than by the use of vision.

The evidence from these experiments indicates that the lower limit of effective vision of the burrowing owl is reached somewhere between a light intensity of 0.000,026 and 0.000,013 foot-candle.

NOCTURNAL ILLUMINATION IN NATURAL HABITATS

The light from the zenithal full moon that falls on the earth on a clear night may be taken as being 0.02 foot-candle. The photometer that I used gave approximately this reading on a bright moonlight night in November, 1939. At quarter-moon the light intensity is reduced to 0.002 foot-candle. Starlight is said to have an intensity of 0.000,08 foot-candle (Smithsonian Institution, 1918: 218).

The light falling on the earth on a moonless night is, however, increased by zodiacal light and by a variable amount of auroral luminosity in the earth's atmosphere. I am informed by Dr. W. C. Rufus, of the University of Michigan Observatory, that the mean value of this light is of the order of five times that of starlight. The total light falling on the earth on a bright moonless night may therefore be estimated to average in the neighborhood of 0.000,4 foot-candle.

On cloudy nights the light falling on the earth is of course considerably reduced in intensity. In order to calculate the amount of this reduction in light intensity I have measured the amount of reduction in photometer readings caused by the presence of clouds in daytime. For this purpose I used a Weston photoelectric exposure meter. A sheet of white typewriter paper was held in the hand and the maximum reading of the light from the

sky reflected from this paper was read on the exposure meter, which was held at a distance of about one foot. Whereas the maximum reading on a sunshiny day in September was 800 foot-candles, that on a cloudy day varied from 80 to 50 foot-candles. This is a reduction to from 1/10th to 1/16th caused by the clouds. On a bright sunshiny day in March the maximum reading of the light reflected from the white paper was 650 foot-candles, while on cloudy days in the same month the readings varied from 50 down to as low as 20 foot-candles. These are reductions to 1/13th down to as much as 1/32nd.

If we assume a reduction in light intensity on a cloudy night of only one-tenth, the intensity falling on the earth under a full moon but with the sky covered by clouds would be 0.002 foot-candle, under a quarter-moon it would be 0.000,2 foot-candle, and on a cloudy, moonless night it would average in the neighborhood of 0.000,04 foot-candle. Under heavy clouds giving a reduction of the light to 1/32nd, the light intensity falling on the earth would be approximately 0.006 foot-candle at full moon but only 0.000,012 foot-candle on a moonless night.

In the habitats in which terrestrial animals live, the light that comes to the earth from the heavenly bodies is usually reduced through the shade cast by various objects, particularly by the vegetation. Under trees that have heavy foliage the reduction in light intensity is considerable. In order to measure the amount of reduction in light intensity caused by the presence of trees I have measured in summer the amount of light reflected from a white paper sheet when held under trees of various kinds compared to that reflected from the same sheet held in open sunlight. A Weston exposure meter was again employed as the measuring instrument.

In moderately dense oak-hickory woods on the George Reserve twenty-five miles northwest of Ann Arbor, Michigan, in September with the trees in full leaf the maximum light reflected from the white paper varied from 16 to 5 foot-candles. At the same time the white paper held in

the open sun reflected 800 foot-candles of light. The reduction in light intensity under the shade of the trees varied therefore from 1/50th to 1/160th. Under a dense clump of shrubs a reading of only 4 foot-candles was obtained, which is a reduction of the light to 1/200th of its value in the open.

Under the shade of deciduous trees in summer, therefore, the light of the full moon would often be reduced to 0.000,2 foot-candle, if we assume a reduction to one per cent. due to the shade. The illumination would be still less than this amount if the shade reduced the light to less than one per cent. On a clear moonless night in summer the light falling on the ground in a deciduous forest would, according to the assumption of a reduction to one per cent., frequently be reduced to 0.000,004 foot-candle or less. On a cloudy, moonless night in summer the light reaching the forest floor must often fall to 0.000,000,4 foot-candle, if we assume a reduction to ten per cent. due to the clouds and to one per cent. of the remainder by the shade cast by the trees. Even less light might be available under a combination of heavy shade and very heavy clouds.

The density of shade in the places where these readings were obtained is by no means the maximum in the oak-hickory habitat. The method used is, however, not suitable for measuring the light intensity in small spaces, such as under the shade of logs or under small clumps of herbs. Nevertheless it is known that rodents and the other small animals that are the prey of owls often hide and travel in these spots of dense shade.

There are of course open spots in most types of forest. In such situations full sunlight may reach the ground at certain times of the day. Readings of the light reflected from the white paper in such sunny spots approached the readings secured outside the forest. Within the forest there is therefore practically complete gradation at different places and at different times from practically full sunlight to dense shade.

Other types of forest are known to produce still more dense shade than the oak-hickory. Grass, herbs, and brush also cast a considerable shade on the ground, though I have made no attempt to measure the amount of light intercepted by such types of vegetation. The light intensity falling on the ground in grass or brush-covered habitats must be intermediate between that in forests and that in completely open habitats.

The shade produced by deciduous trees in summer would seem from the above figures often to reduce the light intensity falling on the ground under the forest to one per cent. or less of that falling on bare ground. When the leaves are off the trees in winter the shade cast by the branches will of course only slightly reduce the light intensity. Coniferous trees undoubtedly cast more heavy shade than do deciduous trees, and because they do not drop their leaves in winter they are effective in reducing the light intensity at all seasons of the year.

The calculations made above are believed to give a rough indication of the amount of light available at night in certain types of habitat. It is not pretended that the figures of possible light intensities arrived at are in any way exact. Certainly there must be much variation from place to place and from time to time in the amount of light that reaches the ground in any given habitat. Also, it is not certain that the reduction in illumination produced by the shade of trees and by the presence of clouds, respectively, can properly be multiplied together as I have done. Furthermore, the light energy measured by the photoelectric cell is perhaps not derived from exactly the same wave lengths as those most used for vision by nocturnal birds and other animals. Nevertheless, it is certain that in some habitats in nature only extremely low intensities of light must at times be available for the use of nocturnal animals.

Discussion

The question may fairly be asked whether in these experiments the owls actually secured the dead mice by the

sense of sight or if some other sense or senses were employed.

It seems unlikely that hearing could have been employed in guiding the owls to their prey, because the mice were dead.

There is the possibility that supersonic sounds given off by the owl may be reflected back from various objects to the ears of the owl and thus enable the animal to learn of the presence of such objects. Such a special sense is suggested by the uncanny ability of most of the owls to fly back to their perch in complete darkness. The only owl that did not show this ability was the burrowing owl and this species very seldom left the ground. The perch in the reaction room was constructed in such a way that it could be approached only by flight. At first, if the light was extinguished when the barred owl or long-eared owl were on the floor of the room, they behaved awkwardly and in the darkness they flew against the sides of the room. Later, however, both of these owls and also the barn owl learned to fly regularly in complete darkness to the floor of the room and back to their perch. This ability, however, may be due to a good sense of position rather than to the perception of supersonic sounds. The fact that all the owls exhibited a greatly decreased ability to secure dead prey in the lowest intensities of light and in darkness, proves that supersonic sounds are at least of no great importance to these owls for finding their prey in dim light.

No evidence is given by these studies that the sense of smell is used by these owls to find their prey. Smell alone is certainly inadequate to enable the owls to locate their prey precisely in very weak light. Otherwise the birds should have been more successful than they were in finding their prey in very dim light and in darkness. In very dim light and in darkness several of the owls at various times actually touched with a wing or stepped upon a mouse carcass without securing it. If these owls use the sense of smell at all in locating the general posi-

tion of their prey its value to them for the purpose must be very slight.

Infra-red rays are presumed to be used by an English species of owl (*Strix aluco*) in finding its prey (Vanderplank, 1934). The North American owls used in the experiments here reported, however, evidently were not able to locate their prey through the perception of infra-red light. Although the mice were freshly killed at the beginning of each experiment and therefore were still warm at that time, the heat rays that they gave off did not enable the owls to secure the carcasses regularly under conditions of very dim light. On one occasion two of the mice placed in the room were by mistake only stunned and were found still alive two and one-half hours later. Yet during this time the barred owl, which was free in the completely darkened room, failed to secure either of them. It seems certain then that infra-red rays are not used by these owls in finding either living or dead prey. These conclusions are in accord with those of Hecht and Pirenne (1940).

It seems necessary to conclude that under the conditions of these experiments the owls must have secured their dead prey largely or entirely by sight, except for the carcasses found by physical contact. Accordingly, the experiments may be assumed to give a rough measure of the ability of the owls to see their prey under various intensities of illumination.

An increase with practice in the ability of the owls to see in very weak light seems suggested in several of the experiments. In several instances the owls made better records in extremely dim lights late in a series of experiments than they had made in somewhat brighter light in the early part of the same series. These improvements, however, may only indicate an increase in the familiarity of the owl with the procedure of the experiment, rather than an actual increase by him in ability to see in weak light. The number of records are in every case few and therefore do not conclusively demonstrate such an increase in the visual ability of the owl with practice.

The experiments here described demonstrate that the barred owl, long-eared owl, and barn owl have somewhat the same lower limit of vision in dim light. All these species seem able to see their prey without difficulty at a distance of six feet or more when the illumination reaching the ground is about 0.000,000,73 foot-candle or more. Below this level of illumination all three species probably have difficulty seeing prey at a distance. Thus, the barred owl was able to pounce directly on her prey when the light intensity falling on the floor of the reaction room was calculated to be 0.000,000,73 foot-candle. But when the light intensity was reduced to 0.000,000,53 foot-candle the bird seemed able to detect the prey only when she was within a foot or so of it. The long-eared owl was able to pounce directly on the dead mouse when the incident light measured 0.000,001,05 foot-candle, but at an intensity of 0.000,000,25 foot-candle he found the carcasses only by searching. The barn owl was undoubtedly able to see objects at a distance of six feet or more at a light intensity of 0.000,002 foot-candle, but he had some difficulty finding the carcasses when the illumination was reduced to 0.000,000,53 foot-candle. The data, therefore, do not demonstrate any very important difference between the ability of these three species of owls to detect prey at a distance of six feet or more.

The ability of the owls to see prey at very close distances in very dim light however, may differ slightly between these three species. It is not certain that the barn owl is able to perceive near-by objects at all at a light intensity of less than 0.000,000,53 foot-candle. The long-eared owl is probably able to perceive near-by objects at least dimly under illuminations as low as 0.000,000,25 foot-candle. The barred owl, when given an abundance of time, may be able to detect near-by dark-colored objects on pale-colored soil under an illumination of as little as 0.000,000,15 foot-candle.

If these figures can be relied upon, the barred owl has a slightly better vision for dim light than the long-eared

owl, and the long-eared owl has slightly better night vision than the barn owl. Such a conclusion would agree with the general observation that the barred owl is an inhabitant of somewhat denser woods as a rule than either the long-eared or barn owls. However, it should be emphasized that the experiments in the dimmer illuminations were much more extensive on the barred owl than on either of the other species. Also it should be repeated that the 20-minute test period mostly used for the barn owl is not fully comparable with the all-night period used with the other owls.

The illumination at which these owls are able to see their prey seems very dim when judged by the human eye. A light intensity of 0.000,000,73 foot-candle falling on the floor of the reaction room would be the amount of illumination produced by a standard candle at a distance of 1,170 feet. Yet these three species of owls were evidently able to see their prey very well at a distance of six feet or more in this amount of light. An illumination of 0.000,000,53 foot-candle would be produced by a standard candle at a distance of 1,374 feet. In such weak illumination these owls seemed still able to see objects that were about one foot away. A standard candle 2,000 feet away gives an illumination of 0.000,000,25 foot-candle, and one 2,582 feet distant produces an illumination of 0.000,000,15 foot-candle. The evidence from these experiments indicates that the barred owl was able sometimes to detect and to secure dead mice in these amounts of light. But in the amount of illumination calculated to be given by a standard candle at 3,536 feet (0.000,000,08 foot-candle) no evidence was found that even the barred owl was able to see anything.

It is not easy to compare the vision of an owl with that of a man. A few observations that attempt such a comparison are, however, here presented. My own eyes, somewhat dark-adapted by a period of five minutes or more in darkness, were able to detect a dead white mouse placed on dark-colored soil on the floor of the reaction

room under an illumination calculated to be 0.000,003,5 foot-candle. At this illumination, however, the outlines of the mouse could not be seen and there was only an indistinct blur of whiteness toward the side of my visual field, even when my eyes were within a few inches of the carcass. I probably would not have discovered the mouse if I had not known exactly where it was. At a slightly lower level of illumination only a faint glow of light could be detected at the edge of my visual field. When the light intensity was increased to a calculated 0.000,015 foot-candle I was able to see the mouse as a white blob. When the illumination was further increased to 0.000,026 foot-candle I was able to see the outlines of the mouse, though still not clearly. Several other persons tested in the reaction room under similar conditions had a lower limit of vision approximately equal to my own. We may therefore conclude that barred, long-eared, and barn owls are able to see objects under an illumination of between one-hundredth and one-tenth of the light intensity that man requires for vision.

This conclusion agrees reasonably well with the calculations of Hecht and Pirenne (1940). From a study of the brightness that produced the minimal effect on the iris of the long-eared owl these authors calculated that this species could see in light 1.5/4.0th that required by man. They, however, agreed that this figure might be off by a factor of 10.

The burrowing owl differs considerably from the other three species of owls tested in its ability to see in dim light. Under the conditions of our experiments the burrowing owls were unable to find dead mice regularly in a light intensity of less than 0.000,026 foot-candle. The burrowing owl, therefore, seems to have somewhat the same ability to see in weak light as does man. It is not nearly so well adapted for vision in dim light as are the other three species of owls under consideration.

This poor adaptation of the burrowing owl for vision in weak light is correlated with its habits. The burrow-

ing owl is much more diurnal in habit than are the other kinds of owls tested. It is not usually active during the brightest part of the day, but it may often be seen moving about in the early morning and in the evening.

Attention has already been called to the fact that the owls seemed able to secure prey somewhat more readily on the pale-colored silica sand than on the darker colored soil. This effect is presumably due to the light reflected from the nearly white silica sand giving a slight increase in overall illumination in that compartment as compared to the compartment with the dark-colored soil.

The computation of the minimum illumination at which the owls were able to find their dead prey has in each case been based on the most favorable conditions. Usually the owls were more successful in securing gray mice on the silica sand than they were in securing ivory or albino or gray mice on the gray gulley soil. The minimum illumination at which the owls would be able to see concealingly colored prey or to find prey of any color on dark-colored soil would undoubtedly be greater than the amounts in foot-candles stated above.

There is a suggestion in some of the experiments that mice having shades of color contrasting with the soil on which they were placed were taken somewhat more readily than those that more closely matched the soil color. These experiments, however, cannot be considered to be a measure of the effectiveness of concealing coloration in protecting these mice from their predators. Such a measure would only be valid if the mice were alive, which these were not. I have, therefore, not made any effort to calculate the proportions of the colors of mice taken on the soils of matching and of contrasting color. Other experiments, designed to measure the effectiveness of the protective coloration of live Peromyscus against owls, are now in progress and will be reported upon later.

The experiments here reported give no information about individual, sexual, or seasonal variation in the ability of owls to see in weak light. Only two burrowing

owls were tested and no attempt was made to separate the records made by each individual. Of the other three kinds of owls studied only a single individual of each species was observed. It is obvious, therefore, that the measurements of light discrimination obtained may not well represent the abilities of other individuals of these species.

Furthermore, additional observations of each of the individual owls studied would have been desirable, especially at the lower light intensities near the critical limit of the owl's vision. However, these experiments are very time-consuming, as will be recognized when it is considered that an average of only about one record can be secured per day. The methods employed are crude and the light intensities could not be controlled fully accurately nor could they be precisely measured. Nevertheless, it is believed that the data presented offer convincing evidence that certain kinds of owls can see their prey in light of extremely low intensity.

The barred, long-eared, and barn owls are in general inhabitants of forest, though some of them at times undoubtedly forage in adjacent open fields. In an earlier section of this report it has been calculated that the amount of light falling on the floor of a deciduous forest in summer may amount to 0.000,004 foot-candle during a clear moonless night in summer. All these owls would be able to see their prey readily in light of that intensity. On cloudy nights, however, the illumination on the floor of a deciduous forest must often fall below 0.000,000,4 foot-candle, and in this light intensity the owls would not be able to see their prey at a distance of more than a few feet at most.

The burrowing owl lives in open fields and makes its home in burrows in the ground. Under heavy clouds on a moonless night the light falling on the earth must nevertheless often be reduced to 0.000,012 foot-candle or less. This is below the limit of illumination at which the burrowing owl can readily see its prey. Furthermore, the

small animals on which the burrowing owl feeds often keep under the shade of grass, herbs, and small shrubs, all of which further reduce the amount of light reaching the ground.

In nature, therefore, all the species of owls must frequently encounter intensities of illumination that are below the minimum at which they are able to see non-moving prey.

Moving animals are more readily detected by sight than non-moving ones, as any field naturalist can attest. It is therefore likely that an owl would be able to preceive living, actively moving prey at a somewhat lower intensity of illumination than the dead prey employed in these laboratory experiments. However, many kinds of animals assume a stationary, rigid attitude ("freeze") when startled or frightened. It may be assumed therefore that an owl, in order to be sure of securing his prey, must be able to see non-moving prey individuals as well as ones in motion. Furthermore, it seems certain that the lower intensities of illumination reached in nature must often extend well below any possible level of owl vision, even for moving objects.

Summary

All four species of owls studied in the laboratory found their dead prey mostly by sight and there was no evidence of their employment for this purpose of infra-red rays or of any senses other than sight and physical contact.

The barred, long-eared, and barn owls are able, under the most favorable conditions, to see and to approach dead prey directly from a distance of six feet or more under an illumination calculated to be as low as 0.000,000,73 foot-candle. When the illumination is reduced to 0.000,000,53 foot-candle, however, all these owls seem to have some difficulty in seeing prey that is more than a foot or so away. There is some evidence that sight may be of some value to the barred owl in finding dark-colored dead prey on nearly white soil at an illumination as dim as 0.000,000,15 foot-candle.

The burrowing owl was unable to find dead prey regularly under illuminations dimmer than about 0.000,026 foot-candle. This species, therefore, has much less ability to see in very dim light than the other three species of owls studied. The burrowing owl, however, is more diurnal in habit than these other owls and also it lives in more open situations.

From measurements of the incident light in nature it is calculated that in the natural habitats of all these owls the intensity of illumination must often fall below the minimum at which the birds can see their prey.

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THE STERILIZING EFFECT OF HIGH TEMPERATURE ON THE MALE GERM-PLASM OF THE YUCCA NIGHT LIZARD, *XANTUSIA VIGILIS*[1, 2]

PROFESSOR RAYMOND B. COWLES AND G. L. BURLESON

DURING the past decade, evidence has been accumulating on a curious phenomenon of thermal differentiation, an apparent conflict between temperatures which may be tolerated or even required by body cells, versus those which may be deleterious to the germ cells.

Most of the earlier work has dealt with the condition as it is encountered in the mammals, but later studies, some of them possibly still inconclusive, are strongly indicative of the possibility that in a majority of the terrestrial animals there may be a similar thermal hiatus between groups of cells.

In every instance so far reported, the body cells of terrestrial animals endure or even require temperatures that are markedly higher than those which can be tolerated by their germ cells. This would seem to be a highly significant phenomenon in view of the fact that there is an almost universal rise in temperature requirements which keeps pace with phylogenetic ascent, and that the either conservative or heat-sensitive germ cells must have kept pace also.

It is well known that in the scrotal mammals, even normal body temperatures are high enough to cause sterility; therefore, by analogy, if parallel conditions existed in any of the cold-blooded animals, optimum temperatures would result in their automatic sterilization. Even less extreme effects resulting from heat sensitivity of the germ cells have dramatic possibilities in connection with the influ-

[1] These investigations were made possible through grants in aid of research provided by the Regents of the University of California.

[2] I wish to express my great appreciation to the junior author who is responsible for all the histological and photographic work involved in the preparation of this paper.—R.B.C.

ence that this trait may have had on evolution, and these possibilities may be enhanced by the comparatively recent discovery (Plough, 1942) that abnormally high but sub-sterilizing temperatures in at least one animal, *Drosophila*, may increase the rate at which mutations appear.

The evolutionary possibilities inherent in this nearly universal duality of thermal requirements have been tentatively presented by Cowles (1944), but while engaged in studies of the available information and the formulation of concepts relative to the effects of thermal problems, it became clear that fuller understanding and added security of conclusions could be obtained only through knowledge of the conditions found in the reptiles. This group of organisms is particularly significant because of their position midway between the aquatic progenitors of land forms, and their ultimate product, the thermally stable warm-blooded birds and mammals.

THE YUCCA NIGHT LIZARD

Xantusia vigilis was chosen as a representative of the Reptilia, in part because of the possibility that only nocturnal or tropical reptiles may have retained the thermal condition most like that of their progenitors, but chiefly because the normal spermatogenic cycle was already available through the work of Miller (1942) and secondarily because of its abundance and availability throughout the year.

As the vernacular name implies, this is a nocturnal lizard with a preferred habitat consisting of groves of Joshua trees (*Yucca brevifolia*) or in some places, stands of the Mojave yucca (*Yucca mojavensis*). More rarely the lizards may be found under the dead leaf rosettes of the Spanish bayonet (*Yucca whipplei*), the Agave (*Agave deserti*) and Nolina (*Nolina parryi*) as well as under flat rocks, especially exfoliating granite. Sometimes it is also found under boards, papers and other trash which has become matted to the ground. Geographically, its range is confined chiefly to the Mojave desert, but to the

southward in California there is a limited extension of its range along the higher flanks of desert mountains.

The adult male lizards average approximately 38 mm, snout to vent, or 70 mm in total length, while the somewhat larger females are approximately 42 mm, snout to vent, or about 85 mm in overall length. Differences in size are neither sufficiently obvious nor constant to afford a ready means for recognition of the sexes. During the spring months, when testicular activity is greatest the femoral pores of the males are enlarged so that they give the legs a somewhat angular cross-sectional outline; nevertheless, even after great care has been exercised in segregating the sexes, a few mistakes will almost inevitably occur.

Adult lizards are always obtainable and there is no evidence of true hibernation, although the congregation of 4 to 8 or more lizards in especially suitable wood-rats' nests[3] suggests that a few individuals may pass into relatively continuous torpor. Most of the lizards seem to remain scattered singly under decaying logs of the Joshua trees, and during spells of warm weather, these animals move out from under the logs and climb up between the trunk and loose bark and foliage. In this manner, these dark-loving lizards can find suitable temperatures during the warmest part of the day, without being exposed to light, and they are thus capable of normal activity even during the relatively cold winters.

These lizards seem to be particularly abundant in the Antelope Valley, a westward extension of the Mojave desert, and in this area winter temperatures often fall to −10° C., sometimes even lower; but these cold intervals are usually short, and the extremes of low temperatures are usually confined to the nights. Even during the coldest weather, the temperature under the logs occupied by the lizards rarely falls lower than 7 to 8° C., and during the daytime, temperatures just beneath the bark of the decaying logs may rise to 20° C., sometimes more.

[3] I am indebted to Mr. Charles Lowe for this information.

Throughout the winter and even as late as April, there are occasional snowstorms or very cold rains that temporarily immobilize the lizards even during daytime. As late as May, night temperatures may fall so low that during the early morning hours the lizards are sluggish.

A body temperature of 0° C. kills these lizards in a few hours' time, but it is probable that only stragglers, or more rarely those living in marginally suitable shelters, suffer from the fatal effects of cold weather.

Laboratory studies of auto-selected temperatures seem to indicate that there is no sharply marked thermal preference, or optimum, within the broad range extending from 25° to 30° C. Temperatures above and below these points seem to be only slightly less satisfactory since the lizards have been observed, apparently at rest, in parts of the experimental cage where air temperatures were as low as 20° C. and as high as 37° C. In one instance three of 20 specimens in a cage were found hiding behind an ice-filled carton where the temperature was 12° C.

An air temperature of 45° C. causes death in 35 minutes, and at the onset of death struggles, thermocouple readings indicated that the body temperature had risen to only 38° C. An environmental temperature of 40° C. causes 50 per cent. mortality within three hours, a notable fact since temperatures from 40° to 45° C. are a daily occurrence in their near-environment from June to late September.

Like all others on which information is available, these lizards are exceedingly susceptible to temperatures only slightly above those which they will tolerate voluntarily, and after they have been removed from their sheltered hiding places it is necessary to protect them from the normal summer heat. Even a relatively short exposure to 39° C. is so rapidly fatal that great care must be exercised to keep them cool, and transportation from the desert to the cooler coastal areas often constitutes a major collecting hazard. If the animals are supplied with drinking water, approximately 50 per cent. will survive 38° C. for a week,

while without water not more than 30 per cent. appear to be capable of enduring the same temperature for only 30 hours. This difference may be due to dehydration resulting from evaporation of moisture used in respiratory cooling activity, or it may be due to either the failure of respiration or of the cooling mechanism when unable to replenish lost moisture. A body temperature of 39° C. can safely be accepted as the lethal temperature.

A week of exposure to environmental temperatures ranging between 37° C. and 37.5° C. killed only apparent weaklings, those with abnormally slender tails or those with a generally emaciated appearance, and we have, repeatedly maintained numbers of the animals for a week or more at 36° to 36.5° C. with no losses.

The experimental animals were supplied with food and water at all times except in the tests reported above. The most successful item of diet was the dry wood termite, *Kalotermes minor*.[4] These were always taken with avidity, as were other, but unidentified species that were only infrequently available. Small larvae of *Tenebrio molitor* were acceptable for short periods, but the lizards soon refused the meal worms. All the animals, including those used in the heat treatment required by the experiments, throve and gained weight. In almost all cases the diameter of the tail increased noticeably, a sure indication of well-being, and on dissection, practically all had large lobules of adipose tissue in the abdominal cavity. Many of the lizards were retained from early April until October 15, and almost all were still in excellent conditions. It is notable as evidence of normal conditions that captive females gave birth to their offspring, both twins and single young, at the same time that freshly captured animals were giving birth to theirs (Cowles, 1944). Both the adults and young showed no effects of the long period of captivity, and they were indistinguishable from the wild stock.

[4] I am indebted to Dr. Gordon H. Ball for the identification of these termites.

NORMAL SPERMATOGENESIS

According to Miller (*supra cit.*) and our own findings, male lizards taken in January show signs of sexual development. This is indicated by the appearance of numbers of mitotic figures in the 3 to 4 rows of peripherally located spermatogonia, and in the 5 to 6 layers of centrally placed spermatocytes. Development throughout February and early March is normally confined to multiplication of these cells, but by late March spermatids are forming. The spermatocytes and spermatids continue to multiply so that by late April only one or two rows of spermatogonia remain, but it is not until mid-May that the spermatids start metamorphosis and transform into the first spermatozoa. By late May the transformation is virtually completed and practically all the cells have reached either the spermatid or spermatozoan stage. Testes remain in this condition until about mid-June, when the initial stage of collapse appears, and by the end of June they are reduced in size and no spermatogenic activity is visible. The testes remain in this inactive state throughout the summer.

Fecundation of the females appears to take place between mid-May and mid-June, and gestation requires approximately 3½ to 4 months (Cowles, *supra cit.*); thus the young are not born until early autumn.

Following the June collapse, the testes remain in a quiescent condition until the following August, when they again show signs of activity as indicated by a notable increase in size which is accompanied by the appearance of numerous mitotic figures, and production of primary and secondary spermatocytes, and what appear to be scattered spermatids. It is possible that a very few spermatozoa might occasionally be produced, nevertheless the testes that we have observed do not appear to reach such a full development as occurs in spring.

Progress toward the development of a fully functional testis may be prevented by the inevitable onset of cold

weather, but in any event no additional growth occurs until the ensuing spring.

The autumnal resurgence in activity appears to be a direct result of moderating summer temperatures, and lengthening of cooling nights and the onset of cold weather, but it is recognized that this may be due to coincidental association of weather and some cyclic phenomenon.

That regeneration is not necessarily a fortuitous juxtaposition of unassociated events is suggested by evidence from other sources such as the studies of Rahn (1940) on the viability of sperms in the uterus of the garter snake *Thamnophis,* and Trapido (1940) on sperm viability in *Storeria.* The observations of Blanchard and Blanchard (1942) on *Thamnophis s. sirtalis* give conclusive evidence for an autumnal resurgence in sexual development in the males, which seems to be postulated on the occurrence of an interval of cold weather followed by Indian summer. Fertile copulations occur, as are demonstrated by birth of normal broods the following spring. There is a strong implication that similar conditions may be found in the desert rattlesnakes, *Crotalus cerastes* and *Crotalus atrox,* as reported by Lowe (1942). These snakes, like*Thamnophis* and *Storeria,* normally breed in the spring of the year.

Experimental Procedure and Results

Testing for the possible existence of thermal divergence was a simple process, since the animals were merely placed in a thermostatically controlled heating chamber and were then allowed to move about within the confines of a smaller centrally placed screened box where previously conducted tests and successive check observations showed fluctuations of only $\pm 0.5°$ C. Because of the nocturnal character of the lizards, a feeble light of 5 cp was employed whenever observations were necessary. Humidity was not controlled, but the animals were provided with a constant supply of water and displayed no signs of discomfort.

No attempts were made to record body temperatures during these experiments, since it was deemed advisable to disturb the lizards as little as possible. Furthermore, previous studies have given satisfactory evidence that these animals are capable of some body cooling, which may amount to as much as 1.5° C. under ideal conditions of high temperature and low humidity. Under no circumstances have body temperatures risen above those of the environment, therefore there was ample assurance that body temperatures would remain at or slightly below those of the testing cage.

Throughout the entire period of investigation extending from January to early May, and from late May to October, 1943, all controls with the exception of sick or feeble animals (about one in fifty) maintained the normal testicular cycle as determined by microscopic sections obtained from wild animals collected at bi-weekly intervals. Control animals were kept in the laboratory at room temperatures ranging between 25° and 27° C. from January until early May when the laboratory temperature rose to 30° – 32° C. for about ten days.

The experiments were designed primarily in order to determine whether or not high temperatures might prevent the production of viable sperm or cause either lasting or transient damage to the spermatogenic organs and mechanism.

In order to exclude the possibility that heat might have less drastic effects at different stages of development it was necessary to discover whether or not heat damage could be produced at any stage of testicular development, particularly during the last stages in the process which occur just prior to the onset of high daytime temperatures and warm night conditions when the temperature of the soil is also rising rapidly.

Additional objectives of these experiments were to discover whether or not heat damage might not be sufficiently transient as to allow rehabilitation and reproduction during the same season, and whether or not collapse

could be prevented or recuperation might not be accelerated by exposure of the animals to low temperatures comparable to those encountered by the animals in nature during winter.

This possibility of recuperation was in part suggested by the work of Wells (1935 a and b) on the thirteen-lined ground squirrel, *Citellus tridecemliniatus,* a seasonal breeder in which normal summer collapse of the testes can be prevented by placing the animal in a cold environment.

In an experiment devised to test these possibilities ten specimens of *Xantusia vigilis* which had been heat-treated and ten which were going through their normal cycle were tested to determine whether low temperatures would prevent immediate collapse of testes in the former and ultimate collapse in the latter. The experiment was a failure; probably due to inadequate facilities for maintenance under the desired conditions which made it necessary to use 12° – 13° C. in place of the needed 15° – 20° C. with interrupted exposure to as much as 27° C. Collapse of the testes was postponed six weeks beyond expectancy, but this may have been due to a retardation of normal progress. It is notable that gravid females maintained during this period under the same conditions as the males all yielded only abnormal embryos.

The effects of treatment at 38° C. for one week result in progressive atrophy and it is doubtful if recovery can take place following such drastic effects as those shown in the sequence of figures in Plate I. The testes show notable signs of extreme damage at the end of the first week of exposure. Most of the spermatogonia and primary spermatocytes characterizing the normal March testis show either agglomeration or disintegration of the nuclear material and macrophage activity is notable. Following the first stages of progressive atrophy the tubules show cloudy degeneration and finally almost complete atrophy sets in.

The effects of 36° C. as applied to the late March testis

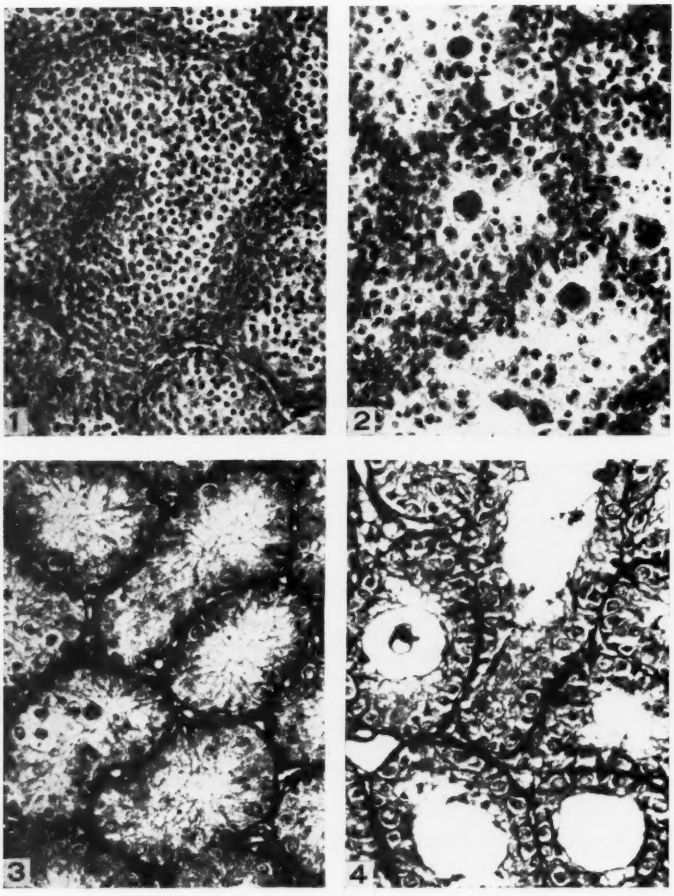


PLATE I. Effects of heat (environmental temperature of 38 ± 0.5 for one week) on early March testis.

FIG. 1. Normal testis. March 8, 1943. ×225.

FIG. 2. Testis after treatment for one week. ×225.

FIG. 3. Testis two weeks after heat treatment. ×225.

FIG. 4. Testis three weeks after heat treatment. Atrophy. ×225.

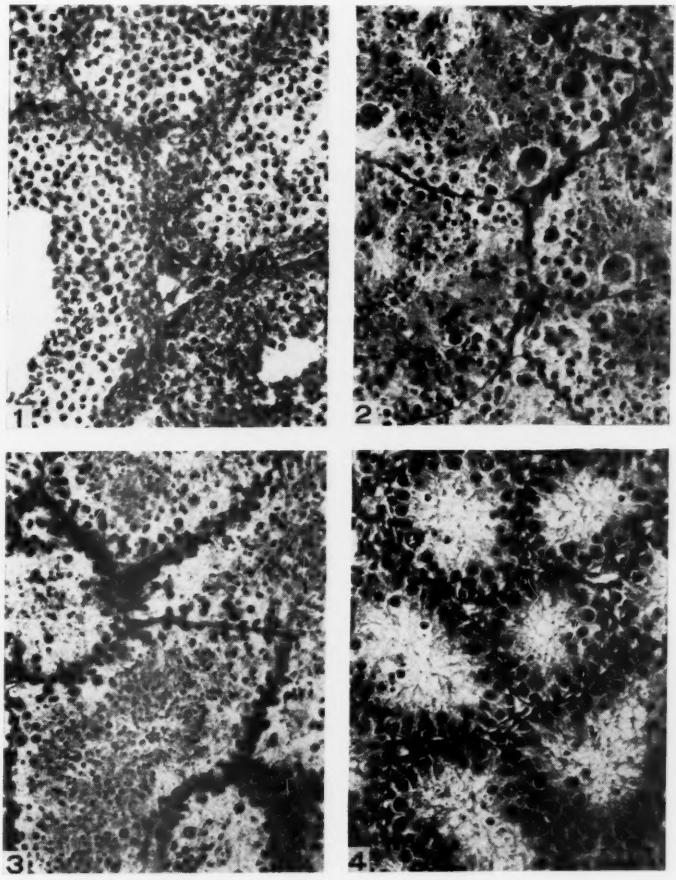


PLATE II. Effects of heat on late March testis, 36 ± 0.5 C. for one week.
FIG. 1. Normal testis. ×225.
FIG. 2. Testis at end of one week. ×225.
FIG. 3. Testis at end of two weeks. ×225.
FIG. 4. Testis at end of three weeks. Recovery. cf. Plate V, fig. 2. ×225.

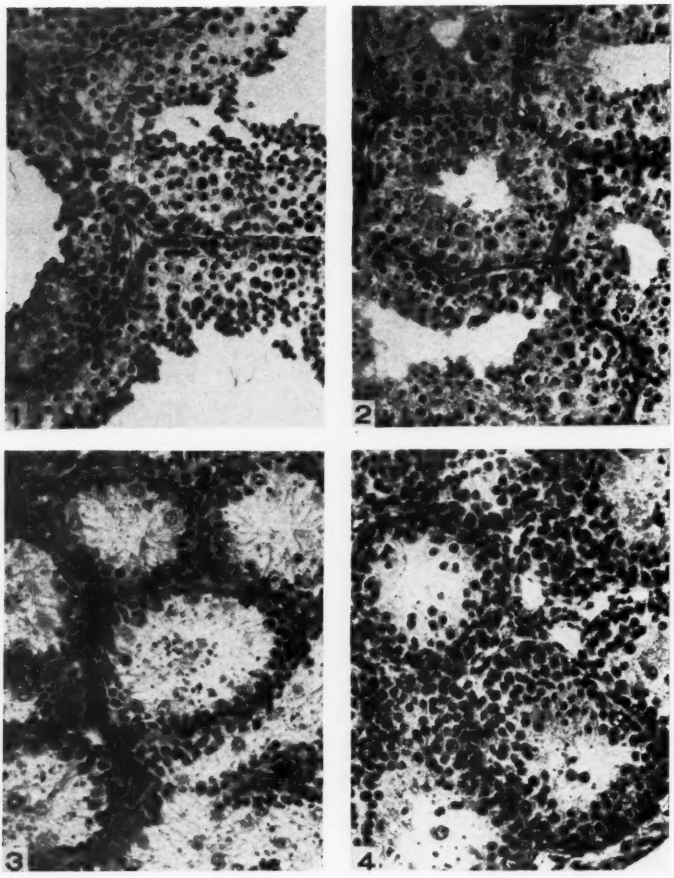


PLATE III. Effects of heat on late April testis, 36 ± 0.5 C. for one week.
FIG. 1. Normal testis. ×225.
FIG. 2. Testis at end of one week. ×225.
FIG. 3. Testis at end of two weeks. ×225.
FIG. 4. Testis at end of three weeks. Recovery, cf. Plate V, fig. 2. ×225.

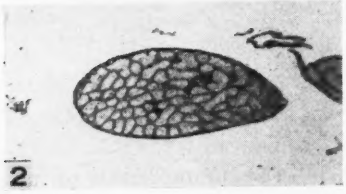
result in extensive destruction of the spermatogonia and disintegration of all the primary spermatocytes. Macrophage activity is conspicuous and, though disintegration is extensive, recovery starts during the third week following heat treatment and the tubules assume the normal summer condition encountered by late June or mid-July. These stages are shown in Plate II, Figs. 1–4.

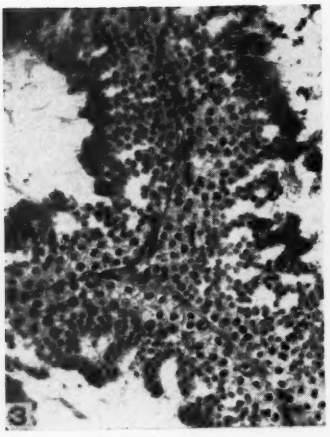
The effects of 36° C. on the late April testis, Plate III, Figs, 1–4, are similar to those of earlier date, but it is notable that the effects of heat are extended to include destruction of the rapidly multiplying spermatids, and secondary spermatocytes, as well as the earlier stages involved in the less advanced testis. Recovery appears to be somewhat more rapid (*cf.* Plate II, Fig. 3), but does not advance beyond the summer state of inactivity, shown in Plate V, Fig. 2.

Even the most advanced stage of testicular development, found in mid-June, suffers from the effects of a week's exposure to a temperature of 36° C. (Plate IV, Figs. 1 and 2, and 3 and 4); but in this case there is a notable inclusion of the transforming spermatids and mature spermatozoa, as well as all the earlier stages in the destructive effects of heat. The gross effects on size of the testes are most clearly observable in Plate IV, Fig. 1, the normal testis and Fig. 2, the shrunken, remains two weeks after treatment. Figs. 3 and 4 illustrate the histolytic effects of heat.

Although the testes of control animals kept at 25° – 27° C. were indistinguishable from those of freshly caught material, a continuous check was carried out in order to avoid any possible errors due to unexpected changes in the controls which might result from the effects of either laboratory temperatures or unusual light or feeding activities.

As long as the temperatures remained 25° – 27° C., no difficulties were encountered, but early in May a hot spell kept laboratory temperatures between 31° C. and 32° C. for almost two weeks. Under these conditions the testes





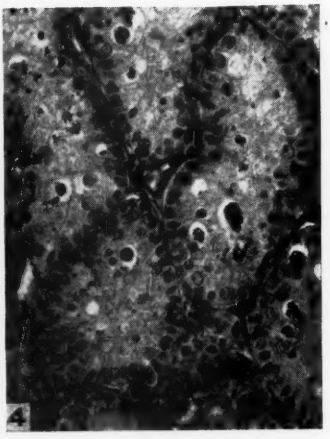


PLATE IV. Effects of heat on mid-June testis, 36 ± 0.5 C. for one week.
FIG. 1. Normal testis at period of maximum development. $\times 33$.
FIG. 2. Heat treated testis showing diminution in size. $\times 33$.
FIG. 3. Histological appearance of testis shown in fig. 1. $\times 225$.
FIG. 4. Histological appearance of testis shown in fig. 2. $\times 225$.

of control animals showed the first signs of abnormality (Plate V, Fig. 1, compared with its freshly caught counterpart, Plate IV, Fig. 3).

There is little reason to doubt that the comparatively moderate temperatures of 31° – 32° C. were responsible for the slight disintegration shown in this control animal, making studies at this level particularly interesting since the lizards are probably subjected to similar temperatures for at least part of the day during late June and early July, the time for normal collapse, and may even come to rest at these temperatures under experimental conditions.

One of the most interesting problems for future investigation is suggested by the possibility that these lizards may either voluntarily or of necessity submit to temperatures that would prevent breeding if encountered earlier in the season.

From May 17 to 24, five individuals were subjected to treatment at 36° C., and these were then kept at room temperatures until August 27, when they were killed and the testes compared with freshly caught material. The result of this experiment is shown in Plate V, Fig. 3, where the experimental testis has shown complete recovery and is no longer distinguishable from the testes of freshly obtained animals, Fig. 4. There can be little doubt but that normal reproductive activity would be possible the ensuing spring.

Discussion

From the foregoing reports on the effects of high temperature on the reproductive cells of the male *Xantusia vigilis* it is apparent that even moderate and somatically harmless heat produces complete sterility, at least for the season in which it occurs. It is not known how permanent the effects of 38° C. may be, nor whether there may be other and more subtle damage at lower levels, but it appears probable that the appreciable and obvious damage resulting from a week of exposure to 36° C. is transi-

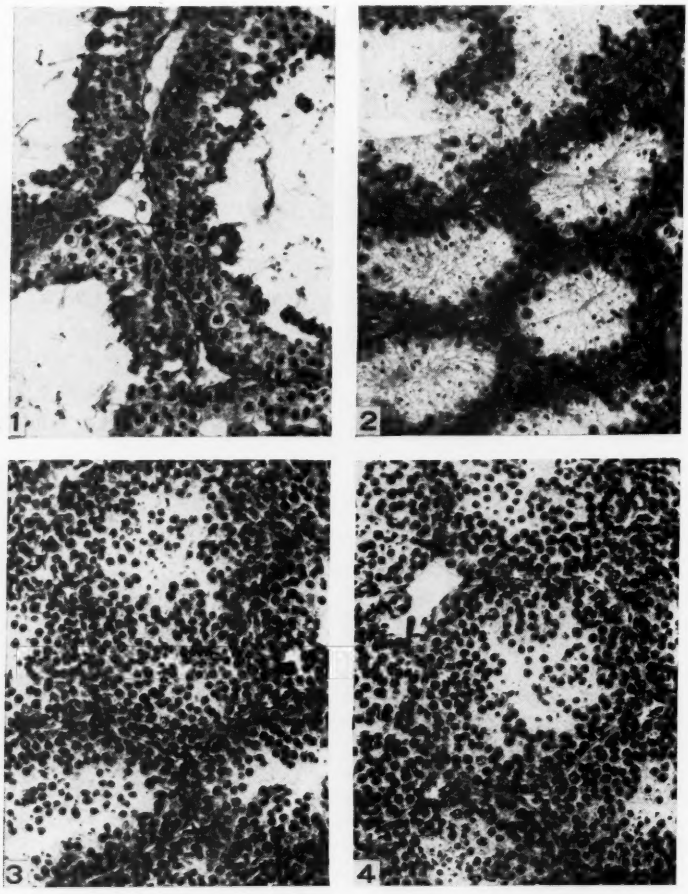


PLATE V. Heat responses of testes of late spring, summer and fall.

FIG. 1. Testis of control killed May 18 after slight heat damage. ×225.

FIG. 2. Normal testis of mid-July for comparison with fig. 1. ×225.

FIG. 3. Recovery of testes treated at 36 May 17–24. August 27. ×225.

FIG. 4. Recovery of testis after normal collapse. August 27. ×225.

tory, and that recovery from the gross effects is completed by the time of normal autumnal testicular resurgence. Whether or not more subtle changes have taken place can only be determined by breeding experiments that may require a number of years for completion.

Because of the universal testicular collapse in nature, and the correlation of this phenomenon with the onset of high summer temperatures, and because of the similarity of normal and experimentally produced failure, it is natural to inquire as to whether or not the strictly seasonal nature of the gonadal cycle may not primarily be due to temperature effects. This view is supported by the autumnal, cool weather, resurgence in *Xantusia vigilis*, and is given additional indirect support by the reports in the previously cited papers of Blanchard and Blanchard, Rahn, Trapido, Lowe and Wells.

The nature of thermal susceptibility is still unknown, but it seems possible that the temperature vulnerability of the male germ cells may be inherent in either the active processes which accompany spermatogenesis, or it may be due to the existence of special properties possessed by these cells only, and not by their somatic vehicle. In this connection it seems particularly significant that some cells, apparently in the peripheral layer of the tubule, the quiescent areas, remain apparently unaffected so far as can be learned, therefore it would appear most probable that vulnerability is associated with rapid cell division. This may be due to a transient difference in the biophysical-biochemical composition of the active cells, or to the over-acceleration of an already superactive process. It is significant that rehabilitation of the tubules comes from the cells which were least active at the time of cellular heat damage.

It is extraordinarily interesting and probably significant that the temperature level affecting the germ cells of one class of organisms does not coincide with that affecting others, but that in each case the level of susceptibility appears to be correlated only with the normal

somatic tolerance of the species. This situation suggests that in the process of evolution and progressive adoption of higher temperatures the male germ cells of each group have been required to make compensatory advances in temperature tolerance in order to keep pace with the advances of the somatic cells. That no animal yet studied appears to have coordinated the temperature limitations of the two groups of cells at present gives the appearance of a reluctant progression in one group and active advances in the other, resulting in an ultimate state of thermal compromise having many trenchant actual and theoretical possibilities.

Because of the possibilities inherent in this phenomenon, it would be desirable to learn whether or not the variations produced by mutations, and necessary for evolution by selective survival, affects the two classes of cells simultaneously, or whether they may be, in a sense, separable. Is there by any chance a separate field of mutations that may adjust the spermatogenic cells and processes to the changes adopted by their somatic vehicle, and have these changes failed to maintain thermal harmony? If this is the case, it would appear that the germ cells must await the remote chance of a purely random mutation leading toward closer thermal harmony, and without this accident the organism must remain the site of a potential conflict of thermal interests, thus existing, in a manner of speaking, in a state of civil war.

Whatever the mechanism may be, it seems to be an inescapable conclusion that the existing, and apparently nearly universal temperature divergence as found in the terrestrial animals must have been involved in the process of evolution on many occasions. The continued existence of many mammals seems to be predicated on the basis of a scrotal or other testicular cooling device, and the mutational steps leading to these developments can not be considered as a simple preordained straightforward progress to this specific solution. The conflicts and difficulties encountered by the reptiles and birds and their solution of them still constitutes an unknown field.

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LIFE TABLES FOR THE BLACK FLOUR BEETLE, *TRIBOLIUM MADENS* CHARP.[1]

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I

ALTHOUGH scattered observations on the life span of many vertebrates and invertebrates are legion, the accurately collected mortality data necessary for the construction of a life table are, apart from man, few indeed. For the insect group, life tables in complete or abridged form have been published for representatives of four orders: the Orthoptera (*Blatta orientalis*), the Lepidoptera (*Telea polyphemis* and *Acrobasis caryae*), the Diptera (*Drosophila melanogaster* and various of its mutants), and the Coleoptera (*Tribolium confusum*). Reference to the first three orders will be found in the papers of Pearl and Miner (1935 and 1936); to the last order in Pearl, Park and Miner (1941). The present paper reports a life table for another, and hitherto little studied, flour beetle, *Tribolium madens*. The details of life table construction, the significance of the life table for many phases of population biology and a review of the literature dealing with mortality in infra-human populations are not considered pertinent for this short paper. If interested, the reader can find further information in Bodenheimer (1938), Dublin and Lotka (1936) and Pearl (1940).

The flour beetles (*Tribolium confusum* and *Tribolium castaneum*) are proving to be appropriate organisms for experimental populations studies (see Ford, 1937, and Park, 1941). It is hoped that, as more background data

[1] I wish to express my sincere thanks to Dr. Alfred J. Lotka, of the Metropolitan Life Insurance Company, whose advice has been invaluable. I am also greatly indebted to Mr. Albert W. Buzicky, of The University of Minnesota, for furnishing me with a culture of *Tribolium madens* as well as for a number of suggestions. This investigation has been aided by a grant from the Dr. Wallace C. and Clara A. Abbott Memorial Fund of the University of Chicago.

accumulate, the black flour beetle (*Tribolium madens*) can be also used in such investigations and the present report is a modest contribution towards that end. There is little information about this species in the literature. Good (1936) notes that it was originally described by Charpentier in 1825 as *Tenebrio madens* and that its present recorded world distribution is western and central Europe, northeast Africa and the United States. In the latter country it is found in certain of the northeastern states, the Great Lakes region, certain of the Rocky Mountain states and the Pacific Coast. It is not reported from South America, Asia and Australia. *Tribolium madens* is clearly less cosmopolitan than either *Tribolium confusum* or *Tribolium castaneum*. Buzicky (1941) discusses its husbandry briefly, and he was well launched on a study of its temperature, moisture and food requirements before his work was interrupted by the war.

The mortality data reported in this paper are obtained in the following way. Two initial cultures are started, one of which contains 125 male imagoes and the other 125 female imagoes. These 250 beetles are within six hours of the same age at the start of the experiment; that is to say, within six hours of eclosion. Each culture container, a standard laboratory finger bowl, is filled with 100 grams of a medium that consists of 95 per cent. whole-wheat flour sifted through number five silk bolting cloth and fortified with 5 per cent. brewers' yeast powder. The two finger bowls are placed in dark incubators at a temperature of 29° C. (with a maximum variation of ± 1°) and at a relative humidity of 60–75 per cent. The containers are not disturbed for five days at which time the medium is poured upon a sheet of paper and the beetles gently removed with a spatula and brush. The number of dead imagoes is recorded and the living forms are returned to their respective dish in 100 grams of fresh medium. This routine is repeated each five days until the last male and the last female dies.

II

The basic biometric constants describing the variation of *Tribolium madens* in respect of duration of life, along with the earlier findings of Pearl, Park and Miner (1941) for *Tribolium confusum* are presented in Table 1. From Table 1 the following points are to be noted:

(1) The mean duration of life for both males and females of *Tribolium madens* is about 220 days or approximately two thirds of a year. This form then, like *Tribolium confusum,* is, for an insect, moderately longevous. Pearl, Park and Miner (1941), however, pointed

TABLE 1

BIOMETRIC CONSTANTS FOR LIFE DURATION OF TRIBOLIUM MADENS (THIS STUDY) COMPARED WITH TRIBOLIUM CONFUSUM (PEARL, PARK AND MINER, 1941)

Species	Sex	Mean (days)	Median (days)	Standard deviation (days)	Coefficient of variability (per cent.)
Tribolium madens	♂♂	199.1 ± 7.64	191.2 ± 9.57	126.7 ± 5.40	63.6
Tribolium madens	♀♀	242.3 ± 7.06	254.5 ± 8.85	117.1 ± 4.99	48.3
Tribolium confusum	♂♂	177.8 ± 2.83	171.6 ± 3.54	84.3 ± 2.00	47.4
Tribolium confusum	♀♀	195.5 ± 3.48	210.7 ± 4.36	103.4 ± 2.46	52.1

out that many beetles have a longer average life duration: a conclusion based largely on the findings of Labitte (1916) who reported mean life durations for 21 species (18 genera) of coleoptera. Of these 21, the longest lived form was *Blaps mortisaga* (914.4 days) and the shortest lived form was *Lucanus cervus* (19.16 days). Fourteen of the male representatives of the species and 16 of the female representatives had a mean life duration exceeding *Tribolium madens,* and seven of the male and five of the female a mean duration less than that of *Tribolium madens.*

(2) The medians do not differ greatly from the means.

(3) Female *Tribolium madens* are longer lived on the average than are males. The mean deficiency in male life duration is $242.3 - 199.1 = 43.2 \pm 10.4$ days, or 17.8 per cent. of the female mean. This difference is 4.1 times its probable error and may be regarded as statistically significant. It is common experience to find that females

have a greater life expectancy than males. This was true for *Tribolium confusum* and has been reported many times for man (Dublin and Lotka, 1936) as well as for a variety of other organisms (Pearl, 1928). It also agrees with the report of Blunck (1924) on *Dytiscus* and of Labitte (1916) on various other species of beetles. In his tabulation the latter author reported only three cases out

TABLE 2

LIFE TABLE FOR MALE TRIBOLIUM MADENS. THE ACTUAL OBSERVATIONS BASED ON 125 IMAGOES

x	l_x	d_x	x	l_x	d_x	x	l_x	d_x	x	l_x	d_x
0–5	125	1	135–140	80	3	270–275	39	1	405–410	7	0
5–10	124	2	140–145	77	1	275–280	38	0	410–415	7	2
10–15	122	4	145–150	76	4	280–285	38	3	415–420	5	0
15–20	118	4	150–155	72	0	285–290	35	2	420–425	5	1
20–25	114	1	155–160	72	1	290–295	33	1	425–430	4	0
25–30	113	0	160–165	71	1	295–300	32	2	430–435	4	0
30–35	113	0	165–170	70	0	300–305	30	1	435–440	4	1
35–40	113	0	170–175	70	1	305–310	29	0	440–445	3	0
40–45	113	5	175–180	69	2	310–315	29	1	445–450	3	0
45–50	108	1	180–185	67	2	315–320	28	3	450–455	3	1
50–55	107	1	185–190	65	2	320–325	25	2	455–460	2	0
55–60	106	1	190–195	63	2	325–330	23	0	460–465	2	0
60–65	105	0	195–200	61	5	330–335	23	0	465–470	2	0
65–70	105	0	200–205	56	1	335–340	23	1	470–475	2	0
70–75	105	1	205–210	55	2	340–345	22	2	475–480	2	1
75–80	104	1	210–215	53	4	345–350	20	0	480–485	1	0
80–85	103	2	215–220	49	3	350–355	20	1	485–490	1	0
85–90	101	1	220–225	46	1	355–360	19	1	490–495	1	0
90–95	100	4	225–230	45	1	360–365	18	1	495–500	1	0
95–100	96	1	230–235	44	2	365–370	17	1	500–505	1	0
100–105	95	1	235–240	42	0	370–375	16	0	505–510	1	0
105–110	94	6	240–245	42	0	375–380	16	2	510–515	1	0
110–115	88	3	245–250	42	0	380–385	14	1	515–520	1	0
115–120	85	4	250–255	42	1	385–390	13	1	520–525	1	0
120–125	81	0	255–260	41	1	390–395	12	2	525–530	1	0
125–130	81	0	260–265	40	0	395–400	10	2	530–535	1	1
130–135	81	1	265–270	40	1	400–405	8	1	535–540	0	..

of 21 in which males had a greater life duration than females.

(4) Under the conditions of these experiments *Tribolium madens* lives longer than *Tribolium confusum*. The mean difference between the males of the two species is 21.3 days and between the females, 43.8 days. The difference for males is not clearly significant, since it has the borderline probability of 8 per cent. The difference for females is decidedly significant ($P = < .07$ per cent.). It cannot be definitely concluded whether the greater length of life of the black flour beetle is the result of genetic (species) or environmental factors. In terms of the latter, the two major experimental differentials be-

tween this study and that of Pearl, Park and Miner are the type of medium and the temperature. In the *Tribolium confusum* case the medium was a patent flour rather than the whole wheat-yeast mixture and the mean temperature was 28° C. rather than 29°.

(5) The differences in variability between both sexes and species are not striking and present no consistent pattern.

The mortality data for *Tribolium madens* are presented in two sets of life tables. The first set (Tables 2 and 3)

TABLE 3

LIFE TABLE FOR FEMALE TRIBOLIUM MADENS. THE ACTUAL OBSERVATIONS BASED ON 125 IMAGOES

x	l_x	d_x	x	l_x	d_x	x	l_x	d_x	x	l_x	d_x
0–5	125	0	130–135	104	5	260–265	58	0	390–395	18	1
5–10	125	0	135–140	99	2	265–270	58	0	395–400	17	1
10–15	125	3	140–145	97	1	270–275	58	0	400–405	16	2
15–20	122	1	145–150	96	3	275–280	58	0	405–410	14	2
20–25	121	1	150–155	93	0	280–285	58	4	410–415	12	1
25–30	120	1	155–160	93	1	285–290	54	8	415–420	11	3
30–35	119	0	160–165	92	3	290–295	46	5	420–425	8	2
35–40	119	1	165–170	89	0	295–300	41	8	425–430	6	1
40–45	118	0	170–175	89	0	300–305	33	1	430–435	5	0
45–50	118	1	175–180	89	0	305–310	32	2	435–440	5	1
50–55	117	1	180–185	89	7	310–315	30	1	440–445	4	1
55–60	116	1	185–190	82	4	315–320	29	1	445–450	3	0
60–65	115	0	190–195	78	0	320–325	28	3	450–455	3	0
65–70	115	2	195–200	78	0	325–330	25	1	455–460	3	0
70–75	113	1	200–205	78	1	330–335	24	0	460–465	3	1
75–80	112	0	205–210	77	1	335–340	24	1	465–470	2	0
80–85	112	0	210–215	76	0	340–345	23	0	470–475	2	0
85–90	112	2	215–220	76	1	345–350	23	1	475–480	2	0
90–95	110	1	220–225	75	1	350–355	22	0	480–485	2	1
95–100	109	2	225–230	74	2	355–360	22	1	485–490	1	0
100–105	107	0	230–235	72	0	360–365	21	0	490–495	1	0
105–110	107	0	235–240	72	1	365–370	21	0	495–500	1	0
110–115	107	0	240–245	71	2	370–375	21	2	500–505	1	0
115–120	107	3	245–250	69	2	375–380	19	1	505–510	1	1
120–125	104	0	250–255	67	5	380–385	18	0	510–515	0	..
125–130	104	0	255–260	62	4	385–390	18	0			

is based on the actual observations of the 125 male and 125 female imagoes. These tables consist of three standard columns: x, age stated as five-day intervals; l_x, the number alive at the beginning of the age interval, and d_x, the number dying during the age interval. The second set of tables (Tables 4 and 5) is computed on the conventional radix of 1,000 rather than 125. In addition to the x column, which is here a 20-day instead of a five-day interval, and the l_x and d_x columns, two other columns are added to these tables. These are the $1{,}000q_x$ column show-

ing the number dying in a particular age interval among 1,000 alive at the beginning of the age interval, and the $\mathring{e}_x$ column showing the mean length of life remaining to each beetle alive at the beginning of the age interval. The l_x items for male and female beetles are graphed in Fig. 1. In all the tables there is a considerable degree of fluctuation in the reported values owing to accidents of sampling

TABLE 4

LIFE TABLE FOR MALE TRIBOLIUM MADENS. COMPUTED ON A RADIX OF 1,000 BEETLES, AND TWENTY-DAY INTERVALS

x	l_x	d_x	1,000 q_x (per 20 days)	e^o_x (days)
0–20	1000	88	88.00	198.40
20–40	912	8	8.77	196.60
40–60	904	64	70.80	178.40
60–80	840	16	19.05	171.20
80–100	824	64	77.67	154.20
100–120	760	112	147.37	146.40
120–140	648	32	49.38	150.00
140–160	616	48	77.92	137.20
160–180	568	32	56.34	128.00
180–200	536	88	164.18	115.00
200–220	448	80	175.57	115.80
220–240	368	32	86.96	118.60
240–260	336	16	47.62	109.00
260–280	320	16	50.00	94.00
280–300	304	64	210.53	78.40
300–320	240	40	166.67	76.60
320–340	200	24	120.00	70.00
340–360	176	32	181.82	58.20
360–380	144	32	222.22	48.80
380–400	112	48	428.57	40.00
400–420	64	24	375.00	42.60
420–440	40	16	400.00	42.00
440–460	24	8	333.33	43.40
460–480	16	8	500.00	40.00
480–500	8	0	0	50.00
500–520	8	0	0	30.00
520–540	8	8	1,000.00	10.00

and it is well to remember that the entries are not smoothed in any way but are computed from the actual observations.

An examination of the tables and figure shows that male *Tribolium madens* have a higher death rate than do females during the first 280 or so days of imaginal life. There are some exceptions to this that undoubtedly represent random fluctuations but, in general, it is true. The greater mean life duration of females is primarily a function of the earlier part of the total life span rather than of later life. This fact is well brought out by the survivorship curves (Fig. 1) from which it is seen that the

TABLE 5

LIFE TABLE FOR FEMALE TRIBOLIUM MADENS. COMPUTED ON A RADIX OF 1,000 BEETLES AND TWENTY-DAY INTERVALS

x	l_x	d_x	1,000 q_x (per 20 days)	e^o_x (days)
0–20	1000	32	32.00	242.40
20–40	968	24	24.79	230.00
40–60	944	24	25.42	215.60
60–80	920	24	26.09	201.00
80–100	896	40	44.64	186.00
100–120	856	24	28.04	174.20
120–140	832	56	67.31	159.00
140–160	776	40	51.55	149.80
160–180	736	24	32.61	137.40
180–200	712	88	123.59	121.60
200–220	624	24	38.46	117.40
220–240	600	32	53.33	101.80
240–260	568	104	183.10	86.80
260–280	464	0	0	84.20
280–300	464	200	431.03	64.20
300–320	264	40	151.51	85.20
320–340	224	40	178.57	78.60
340–360	184	16	86.96	73.40
360–380	168	24	142.86	59.60
380–400	144	16	111.11	47.80
400–420	128	64	500.00	32.40
420–440	64	32	500.00	35.00
440–460	32	8	250.00	40.00
460–480	24	8	333.33	30.00
480–500	16	8	500.00	20.00
500–520	8	8	1,000.00	10.00

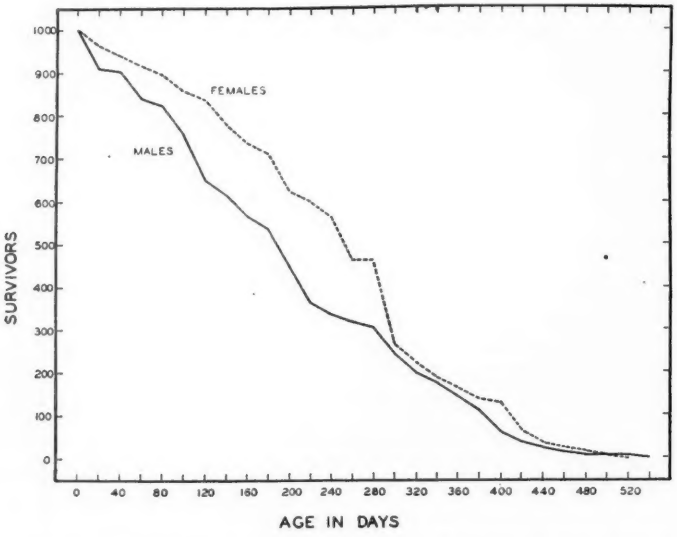

FIG. 1. Survivorship curves for male and female *Tribolium madens* (radix of 1,000 imagoes).

two lines start from the same point, begin to diverge almost immediately, and remain far apart until about 300 days. Thereafter, the differences between them are probably of no great moment. The $\mathring{e}_x$ columns show that the life expectation is consistently greater for females until 220 days, after which there is a strong similarity between the sexes.

Although there are some minor differences in mortality between *Tribolium madens* and *Tribolium confusum*, the basic pattern is fundamentally similar. Both exhibit considerable mortality during early imaginal life (0–60 days) with a steady reduction in survivors thereafter until late in life (380–400 days) after which a few longevous male and female beetles linger on for 100 or so days. In both species the male sex actually has a longer total life span than the female despite the fact that its average duration is decidedly less. It is not certain whether this represents a real sexual difference or is merely a happenstance.

There are some interesting similarities between the survivorship curves of the genus *Tribolium* and those of man. This similarity is more striking perhaps for *Tribolium confusum* than for *Tribolium madens*, but it does exist for the latter species also. The question has been discussed in detail elsewhere (Pearl, Park and Miner, 1941) and the reader is referred to that source if interested.

III

In this paper are presented life tables for males and for females of the black flour beetle *Tribolium madens* Charp., living in regularly renewed flour-yeast medium under favorable laboratory conditions. These mortality data are discussed and compared with those collected earlier for the confused flour beetle *Tribolium confusum*. The latter species along with *Tribolium castaneum* are appropriate, and much studied, organisms for the analysis of experimental population problems. It is hoped that *Tribolium madens*, the subject of this paper, will also

prove helpful in this connection, and the object of the present study is to place on record certain basic observations which can be used in later investigations.

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THE RELATIONSHIP BETWEEN SERIAL AND SPECIAL HOMOLOGY AND ORGANIC SIMILARITIES

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INTRODUCTION

IN a critical review of the history of the concept of homology Boyden (1943) takes the view that serial and special homology "have an almost totally unlike significance to the zoologist." He would therefore limit the word homology to Owen's earliest and narrowest definition (which Owen himself later felt compelled to broaden very greatly). Under that original definition homologies exist only between special organs, *e.g.*, vertebrate fore limbs, in a number of different kinds of animals. For the similarities between structures within a single individual, *e.g.*, the fore and hind limbs, Boyden would substitute the old term "homotypy" in place of the commonly used "serial homology." Even such a case as the Drosophila mutant *proboscipedia* in which tarsi-like structures appear on the proboscis does not, according to this view, indicate any serial homology between structures on the same individual, because "the original tarsi still occupy their normal position on the legs."

The contrary view, that there is but one kind of homology of which both serial and special homology are merely aspects, has been strongly supported by Bateson (1894) in his work on variation, and by Hubbs (1944) in his critique of homology and analogy. Hubbs points out that once you admit the homology between any scale x of a trout and any scale y of a salmon, and between this scale y of the salmon and scale z of the trout, then it is logically impossible to deny a homology between scales x and z on the trout. As Bateson put it, "No one has proposed to homologize single leaves of one tree with single leaves on another; it is not expected that the separate teeth of a Roach have definite homologies with separate teeth of a Dace. . . . But in a series whose members

are differentiated from each other the existence of such individuality is nevertheless assumed."

HOMOLOGY IN MORE AND IN LESS SPECIALIZED ORGANISMS

The possibility then presents itself that the difference in viewpoint just indicated is largely a reflection of the fact that some investigators focus their attentions chiefly on highly specialized organisms like the mammals or the insects, while others look at less specialized groups. In mammals a one to one correspondence between many special structures appears very evident. All mammals (with nevertheless two or three exceptions) have exactly seven cervical vertebrae. Thus a one to one correspondence between them seems plausible. But even here, if other groups of vertebrates are included, insurmountable difficulties arise. For example, in the words of Bateson, "Which vertebra of a Pigeon, which has fifteen cervical vertebrae, is homologous with the first dorsal of a Swan which has twenty-six?"

Among less specialized organisms Boyden himself comes very close to agreeing that only an arbitrary distinction can be made between special and serial homology. In his consideration of tapeworms Boyden holds that, "Whether the corresponding organs of each proglottid are homologous or homotypic depends on whether one views the tapeworm as a colony or as a single individual." An even clearer case, if that be possible, is to be found in the various freshwater Oligochaetes that reproduce by fission. In a worm like Dero or Nais it is possible to equate a nephridium or any other organ of a given segment, say the fifteenth, with the same organ of the fifteenth segment of another worm. However, when one of these worms reproduces by breaking into two, it usually happens that the nephridia that were in the fifteenth segment of the original individual come to lie in one of the anterior segments, say the sixth, of one of the two new worms. Furthermore, it is possible to vary at will, by controlling the temperature and food supply, the segment of the new individual in which the old nephridia will be.

Thus conditions can be so arranged that the organs in the fifteenth segments of several worms will come to lie, after fission, in the sixth, eighth and ninth segments of the new worms (Van Cleave, 1937).

Two questions at once arise. Is an organ, originally in the fifteenth segment but now in the sixth, homologous with itself of an hour or so earlier when it was in the fifteenth segment? Secondly, are two similar organs, originally in the fifteenth segments of two different worms, no longer homologous with each other now that one has come to be in the sixth and the other in the eighth segment of the new individuals? Perhaps answers can be given to these questions and a clear distinction still maintained between serial and special homology. But from the standpoint of developmental mechanics the questions themselves present no puzzle because they are seen to be essentially meaningless. Before considering the developmental point of view, it should be mentioned that comparable questions arise concerning the relationships of the tentacles in medusae and polyps of the same species of Coelenterate, or the relationships between various structures in Siphonophores, or in the various generations of a single species of Trematode.

Homology and Developmental Mechanics

The findings of developmental mechanics are discussed briefly by Hubbs (1944) who throws out the suggestion that these considerations add to the "difficulties" and "complications" of the situation. However, viewed from a slightly different angle, it seems even truer that the concepts of developmental genetics and experimental embryology (if these are indeed not the same thing) simplify rather than complicate these problems.

All will agree that every organism and every structure within an organism is the resultant of the action and interaction of the genes and their products within a particular environment. Under ordinary circumstances the dominating environment for any cell in a developing animal or plant is all the other cells of the embryo, in

other words, the organizers of the first and second orders, the fields, gradients, hormones and other influences that may arise as a result of the action of the gene complex of the zygote. Furthermore, the constellation of gene activities primarily concerned with the formation of limbs or any other structures will produce one end result in one developmental environment and some other end result, more or less different, in some changed developmental environment. Likewise, when the developmental environment remains essentially unchanged while one or more of the specific genes becomes altered, a somewhat different end result will be produced. In general, similar developmental forces produce similar end results.

On this basis both serial and special homologies as well as the general homologies seen in feathers, scales and leaves are all the expressions of similar developmental forces. Sometimes these similar developmental forces have acted within several different kinds of animals or plants, sometimes within different parts of a single individual. Exceptions to this rule will be discussed later, but this is apparently true of the great mass of similarities between organisms to which the word homology is usually applied. In phylogenetically related species, all homologies, serial and special alike, go back to ancestral similarities, ultimately to identities, with possible exceptions to be noted later.

To illustrate with a familiar specific case, all the appendages of the ancient Trilobites were biramous and identical or nearly so, from head to tail. According to the view outlined above, all the appendages were anatomically the same because they were all due to the same developmental causes. So to-day all the nephridia of an annelid or the scales of certain fish or the leaves of trees are alike for the same reason—similar developmental causes. During the evolution of the Arthropods from the Trilobite-like ancestor into all the various species of the modern Crustacea several possibilities present themselves. Genes may have changed in such ways that it then made a difference whether the limb primordium

developed at the anterior or the posterior end of the animal or at some intermediate level. Consequently, the appendages found at the different levels of the body came to differ from each other. In different lines of descent these changes must have been different. Thus different species have appeared with appendages modified in different ways. One and the same process, in fact one and the same mutation can thus have led simultaneously to the differences that are recognized between serially homologous and specially homologous structures. In any specific case it may have been gene activities chiefly concerned with the development of the limb anlagen that underwent most of the changing, or it may have been the gene activities primarily concerned with the general embryonic environment. Over a period of time both were probably involved.

Developmental forces that would fit into a picture of this kind are well known. A large proportion of the known gene mutations appear to affect some particular structure in a highly localized and specific manner. The eyes, wings, horns or perhaps particular bristles are changed while all the rest of the organism seems at least to be untouched. But a great many gene changes have been observed that are general in their effects. Such gene changes alter the growth of hair or feathers on every part of the body, change the amount of pigment deposited throughout the organism or are responsible for other results not limited to a localized structure. Turning to directly observable developmental forces, there are the ubiquitous metabolic gradients so long studied by Child and his school. Cases are known in Amphibia where head ectoderm possesses very different developmental potencies from ectoderm taken from more posterior regions. For example, gill-forming mesoderm will form a gill if overlain with any head ectoderm. If it is covered with ectoderm from flank, the formation of a gill is suppressed (Severinghaus, 1930).

The theory developed by Goldschmidt (1940) to account for homeosis in Drosophila also fits into this scheme

nicely. In the case of *aristopedia* in which the antennae are replaced by the tarsus of the leg, it had been found by Balkaschina (1929) that normally the imaginal discs for the legs develop and differentiate before those for the antennae but that in *aristopedia* the imaginal discs for the antennae develop at the same time as those for the legs and develop as legs from the beginning. Goldschmidt's explanation runs approximately as follows. The anlagen or imaginal discs for all the appendages are at first identical in potency. The kind of structure each develops into depends on the embryonic environment at the time of its development. The developmental forces, probably largely determining substances, within the embryo change with a definite velocity and in a definite order during the course of embryogenesis and later development. All imaginal discs that develop simultaneously are in a plastic condition at the same time and therefore come under the same determining influences and develop into the same structures. Any influence that changes the rate of development of an imaginal disc automatically changes the developmental forces presiding over its differentiation and consequently changes the ultimate structure formed. Presumably it would also be possible that some change could take place in the nature of the discs so that they would respond or fail to respond in new and different ways to the same sequence of developmental conditions.

A simple but illuminating situation is found in the Siamese cat and in the Himalayan rabbit (Iljin, 1931). In these animals all the hairs are light tan (in the cat) or white (in the rabbit) if they develop at any point on the skin where the temperature is above a certain critical level. Wherever the skin temperature falls below that level, as it does on the tips of the ears, nose, feet and tail, the hairs that develop are black. Experimentally it is possible to increase the area of black hairs until it covers the entire body by allowing the hairs to grow out at abnormally low temperatures. Likewise the area of tan or white hairs can be increased by raising the tem-

perature of the room in which the animal lives during hair growth. Similar changes in the area of pigmentation can be produced at will by raising or lowering the thyroxin level in the animal. It is possible to imagine related species in which the skin all over the body is above the critical threshold temperature and which is consequently completely white, or a related species in which the skin for some reason, perhaps hormonal, is everywhere below the critical level and which is consequently all black. Clearly, from the developmental point of view, most of the similarities or homologies, whether between structures in different species or in different parts of the same species, *i.e.*, whether special, serial or general, are all similar because due to similar developmental forces.

One of the results of this concept of homology is that it renders it unnecessary, in fact meaningless, to talk about "moving" the tarsi or any other structures from one level of the body to another. When the total area of black hairs is increased by allowing the hairs to develop in the cold, black hairs are not "moved" from the tips of the ears to their bases. Obviously enough, the developmental conditions have so changed that in respect to pigment formation the situation at the bases of the ears has become like that at their tips. Just so when tarsi appear in the mouth region, or the eye becomes an antenna, it is irrelevant to ask whether or not the "original" tarsi or the "original" antennae are still in their usual positions. If the tarsi are still found in their usual place, that would merely indicate that the change which brought about their development in a new location was not accompanied by some condition which inhibited their development in the old. Contrariwise, if the tarsi are no longer present in their old site, it merely indicates that the change was accompanied by some inhibitory factor.

It is tempting to compare what is now known about the interaction of developmental forces with Owen's theory that the form of any animal is the result of the interplay of what he termed an "all-pervading polarizing force" and a "special organizing force." Doubtless there is a

certain rather vague correspondence between these concepts and present ideas about primordia, fields, gradients, organizers and gene action, although Owen lacked all the concrete information now available. Certainly if there is to be any return, as has been suggested, to Owen's ideas, it will have to be to his often neglected suggestions of developmental forces and to his later and most general conception of homology rather than to his first and narrowest.

HOMOLOGY AND SIMILARITY

It is important to remember that the general principle stated at the beginning of the previous section, *i.e.*, from the developmental point of view all homologies whether special or serial are the expressions of similar developmental forces acting sometimes in different kinds of animals, sometimes in different parts of the same animal and tracing back to ancestral identities, is a principle that is only true among related organisms and not always true even there. Moreover, the term developmental forces is such a broad term that it demands further definition. As de Beer (1938) has made quite clear, "characters controlled by identical genes are not necessarily homologous" and likewise "homologous characters need not be controlled by identical genes." Among other examples he cites a single gene in poultry that controls both the formation of a crest of feathers and the formation of a cerebral hernia. Despite the fact that they are both controlled by a single gene, no one would suggest a homology between two such diverse structures. De Beer also cites the way eyes may be made to reappear in homozygous "eyeless" stocks by reshuffling the gene complex in such a way that other genes can "deputize" for the normal allele of the "eyeless" gene. Since even when homologous characters are identical in structure they need not be controlled by identical genes, de Beer concludes, "it is likely that when homologous characters do not resemble one another closely the genes controlling them may be very diverse." Of course a certain amount of diversity must exist or the resulting developmental forces and consequent final structures would be identical.

In the end the concept of homology will probably undergo the same kind of development that many other scientific concepts have undergone. As every one knows, originally all differences from the norm for a group were lumped together simply as "variations." Now it is clear that variation includes at least two very different kinds of events—hereditary and non-hereditary variations. In a similar way homology may continue to be a useful word to denote correspondences between different organisms or different parts of the same organism. But with the growth of genetical and embryological knowledge it is becoming increasingly evident that the homologies or, better, the similarities between organisms or their parts are of several different kinds.

Perhaps it would be well to discard the word homology altogether and to substitute the neutral descriptive term, similarity. Is not "homology" something of a straw man? A group of calendar reformers who set out to ask how many days there "really" are in a week would obviously be ridiculous. Are biologists who ask what homology "really" is, very different? At best homology means some kind of similarity, and of organic similarity there are various kinds.

Among organic similarities the basic distinctions are not between serial, special and general homologies because these in fact can not be distinguished unless attention is focused on a few limited cases. The basic distinctions among the similarities of plants and animals would rather seem to be those based on (1) developmental, (2) genetical and (3) evolutionary differences. Thus some similarities are the result of similar developmental forces, while other similarities (probably much rarer) are the result of quite different developmental forces. The former may be termed homodynamic, the latter heterodynamic similarities. Some similarities are the result of variations on a common basic gene complex, while other similarities arise as "convergent" variations on radically different gene complexes. These may be called homogenetic and heterogenetic similarities respectively. For the similarities that trace back to a common

ancestor the word homophyletic suggests itself; for those that do not trace back to a common ancestor the word heterophyletic. Consequently, with three pairs of alternatives there are eight theoretically possible categories of similarities.

Most of the similarities to which the word homology is commonly applied are apparently homophyletic, homogenetic and homodynamic. Here belong the familiar similarities between the limbs of vertebrates or the scales of fish. For a tremendous number of cases, however, not enough is yet known about the evolution, the genetic basis or the embryological factors concerned to be able to say with any assurance what kind of similarity is present. For example, this is certainly true of the concentric circles of pigment that are so frequently found in the wings of butterflies and moths, the feathers of birds and the skin of fish, salamanders, and reptiles. A like ignorance surrounds the striking similarities between the eyes and also the mouth parts of certain molluscs and vertebrates. Some of these instances, especially the concentric rings of pigment, would appear at least to be due to closely similar developmental forces, *i.e.*, to be homodynamic. At the same time, since they are in such very diverse kinds of animals, most of these cases probably arise from very different gene complexes. Most certainly, in the case of the butterflies and the fish, the similarities are not historically connected in the actual course of evolution. Consequently, these particular likenesses would seem to be homodynamic but heterogenetic and heterophyletic. All this is of course as yet speculation.

CONCLUSION

As Bateson and Hubbs have both demonstrated, the distinction between special, serial, and general homology is not a valid one. This becomes clear as soon as attention is shifted from the limited cases found in highly specialized organisms to the more general situation represented by the scales of fish or the vertebrae of birds. From the standpoint of developmental mechanics, most of the similarities whether called special, serial or general

homologies are all alike the end result of similar developmental forces acting sometimes in different parts of a single individual, sometimes in individuals of different species. Very often these similarities trace back to ancestral identities.

The word homology had perhaps best be discarded as too charged with metaphysical overtones and a neutral descriptive term like similarity substituted.

The basic distinctions between the similarities shown by animals and plants would seem to be those based on (1) developmental, (2) genetic and (3) evolutionary differences. Similarities due to similar developmental forces may be called homodynamic, those arising from different developmental forces, heterodynamic. Similarities arising out of variations on a common gene complex may be termed homogenetic, those arising from radically different gene complexes, heterogenetic. Likewise any similarities that are derived from a common ancestor may be called homophyletic, those not so derived, heterophyletic. Thus eight different categories of organic similarities are theoretically possible.

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ON PARTIAL MELANISM ASSOCIATED WITH PARATHYROID ENLARGEMENT IN PIGEONS

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MELANISM arising from physiological disturbance has not previously been reported for domestic pigeons. A few cases of partial melanism have been observed in the pigeon colony of this department under circumstances which suggest the nature of the factors intimately associated with the belated appearance of this condition. It has been found that, on the diet supplied to birds of this colony, a deficiency of sunlight regularly leads to enlargement of the parathyroids and also seems to be concerned in the occasional onset of partial melanism. Since we do not plan a further study of this type of melanism it seems useful to record these observations in connection with data showing the relation of sunlight to parathyroid enlargement and rickets in pigeons.

Black pigeons are of course quite common, and this and other hereditary types which might be mistaken for "physiological" melanism have been studied fairly extensively (Hollander, 1938); such types are not considered here. Also excluded are genetic mosaic effects (aberrantly colored patches of plumage or black flecks and streaks in feathers or piebaldness) which are fairly well understood (Hollander, 1944). The melanism reported here had the following characteristics: (*a*) it was observed only in adult female pigeons of essentially wild-type coloration—gray-blue with black bands on tail and wings; (*b*) it was definitely partial rather than complete melanism; (*c*) it first appeared after one or more moults; (*d*) when the blackening did not involve entire feathers it produced transverse bands on the feathers, not longitudinal streaks typical of mosaic effects.

Cases of Melanism

The first specimen, E149, was noted to have melanistic feathers scattered among gray-blue ones when she came to autopsy at the age of 4 years (Fig. 1, *C*). This bird had been breeding, though not very successfully, and for some weeks had been ill; one wing was lame, probably from a disease (paratyphoid) which commonly produces this condition. The only unusual finding at autopsy was a yellow tumor-like body (weighing approximately 50 mg) adjacent to the right thyroid gland. This body was sectioned (by Miss V. M. Rauch) and identified as parathyroid tissue.

Four other domestic pigeons showed melanistic feathers, more particularly on the rump and breast. Two of these cases (Nos. X566 and X177) have been killed. No. X566, aged 16 months, had been ill and emaciated for some weeks; the parathyroids were not weighed but were rated as three to four times normal size. No. X177 was killed at 30 months in apparently healthy condition; the four parathyroids weighed 16 mg, and the autopsy showed no other marked deviation from normal. The other two females, X803, X899, are still alive (Fig. 1, *A* and *B*); they were biopsied when 12 and 13 months old, respectively, and their parathyroids were estimated at about six and four times the normal weight. The three females last described had remained in fair or good health; they had produced fair numbers of eggs and their bones were not obviously softened. All the melanistic pigeons were kept and bred in cages with exceptionally little exposure to light during many months before the melanism was observed. Although a glass side of their colony house was removed during the summer, these birds were then exposed to very little direct sunlight.

An informative though indecisive test was made on two of the melanistic pigeons (X803 and X899) listed above. Immediately following the biopsies on their parathyroids these birds were fed a single capsule of concentrate (1800 I.U. of vitamin D; 15,000 I.U. of vitamin A) of cod-liver

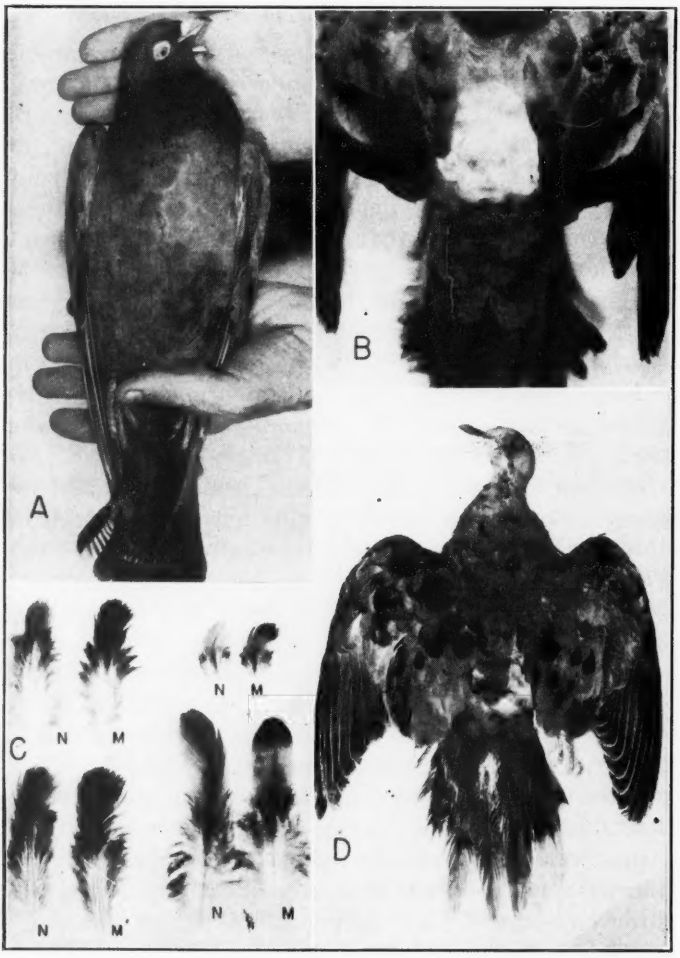

FIG. 1. A. Ventral view of ♀X899. Most of the visible breast plumage shows partial melanism; the patch of normal plumage on the anterior left breast of the bird was grown following administration of cod-liver oil concentrate. B. Dorsal view of ♀X899 showing many melanistic feathers. C. Pairs of adjacent normal (n) and melanized (m) feathers plucked from ♀E149. D. Dorsal view of preserved skin of hybrid dove, ♂D918, showing scattered melanistic feathers, especially in left-wing coverts.

oil. The new breast feathers which grew over the site of the operation were not melanistic (Fig. 1, *A*). Since no control is available one must admit the possibility that the oil (vitamins D and A) was not responsible, but the result does conform with the view that this type of melanism is connected with vitamin-D (light) deficiency.

A sixth case of melanism occurred in a hybrid dove (D918) (derived from *Zenaida vinaceo-rufa* and *Zenaidura carolinensis*). This male dove was very old (18.1 years) at death. During at least the final five years of its life it was unable to fly, and some melanism was present during much or most of this period. Some black spots, restricted to certain feathers of the wings, are normal in these birds. For at least two years before its death some black feathers were scattered throughout its plumage along with other feathers of normal or nearly normal color (see Fig. 1, *D*). This bird was exposed to some direct sunlight during summers only; its inability to fly, however, forced it to live on the floor of its cage where light was most restricted. At autopsy the parathyroids of this small (140 gm) bird weighed approximately 18 mg.

Parathyroids and Rickets

During recent years parathyroid enlargement has been observed rather frequently in pigeons of this colony, more especially in squabs with pronounced rickets and occasionally in adult breeding females with osteomalacia. In such pigeons the parathyroids sometimes weighed almost as much as the thyroids; values of 20 to 35 mg (total for 4 glands) were not rare. Deficiency of vitamin D and sunlight almost certainly induced this enlargement of the parathyroids and the frequently associated defective ossification of the bones. The occurrence of enlarged parathyroids and soft bones was known to be limited to birds reared or kept in cages where little or no ultraviolet light entered. The diet of those birds was not

fortified with vitamin D.[1] On the same diet, and with direct sunlight, no pigeons have been found with parathyroid enlargement.

Within the past year several of these birds with soft bones have been killed at various stages of immaturity. The weight of the parathyroids of these birds was obtained, and records made of the light conditions in the cages in which such birds were reared. Similar weights

TABLE 1

WEIGHTS OF PARATHYROIDS OF PIGEONS IN RELATION TO DEFECTIVE OSSIFICATION AND DEGREE OF EXPOSURE TO DIRECT SUNLIGHT

Condition of keel and femur	Age	Degree of exposure to sunlight	Date	Sex and number	Weight of parathyroids			Body weight avg.
					Minimum	Maximum	Average	
	mos.				mg.	mg.	mg.	mg.
Soft	2.8	Slight	4/27	♂♀6	20.3	35.0	28.5	239
Normal	2.7	Slight	5/8	♂♀7	5.0	10.1	7.4	298
Soft	2.0	Slight	5/15	♀3	16.0	18.4	17.2	228
Normal	3.1	Slight	5/15	♂3	6.9	9.7	8.5	320
Soft*	1.3	Slight*	5/6	♂♀3	8.8	17.4	12.3	(200)
Normal	1.1	Slight	6/21	♂1			5.9	230
Normal	2.0	Complete	7/25	♂♀6	1.8	4.3	3.4	321
Normal[1]	23.5	Complete[1]	8/8	♂♀5	3.4	4.2	3.7	390
Normal[2]	2.7	Complete	8/15	♂♀11	1.7	4.8	3.3	(430)
Soft keel[3]	31.0	Slight	7/25	♀1			27.8	251

* Young and parents both subjected to a low calcium diet (corn, Kafir and salt; no grit except sand) and to no direct sunlight.

[1] During the previous 3 months these birds were exposed to direct sunlight during several hours daily.

[2] Birds of a large breed (Carneau) injected daily for 15 days (dihydrotachysterol, estradiol or fed aluminum hydroxide) before measurement.

[3] Apparently a case of acute osteomalacia, but femur nearly normal; killed 3 days after laying egg.

and records were obtained for other birds which, though reared under similar conditions of lighting, showed no obvious softening of the bones. Still other normal young, hatched and reared in cages exposed daily to some hours of direct sunlight (after removal of glass sides from the colony houses on May 10), were killed (July, August) in order to obtain adequate control data for both of the preceding groups. Data obtained from those three types of

[1] The chief source of traces of vitamni D in the feed would probably be Kafir (or milo). These grains ripen under partial exposure to sunlight. The other ingredients of the diet were cracked yellow corn, wheat and peas. The commercial grit kept before these birds contained oyster shell, calcite, sand, salt, charcoal and Venetian red.

young are given in Table 1. Some data for adults are included in the tabulation. It will be observed that the weight of the parathyroids of either young or old pigeons which had been exposed daily for some months to direct sunlight ranged from 2 to 5 mg. Young reared in relatively dark cages (and behind glass) showed two grades of parathyroid enlargement. Those with soft keels and femurs had extremely enlarged parathyroids, while those without obvious bone defects had parathyroids only about double normal size. However, one squab reared in the sunlight on a calcium-deficient diet developed severe rickets with little or no parathyroid enlargement, while three other young on a calcium deficient diet in the absence of direct sunlight showed some enlargement of the parathyroids (Table 1).

Discussion

Higgins and Sheard (1928) reviewed the earlier literature and also carefully tested the relation of light rays and vitamin D deficiency to parathyroid enlargement in chickens. They concluded that vitamin D deficiency causes the parathyroid enlargement. Oberling and Guerin (1934) later reported, on the basis of evidence very inadequately described, that not vitamin D but a mineral deficiency is the cause of parathyroid enlargement. Doyle (1925) described rickets in mature laying fowl and noted its association with parathyroid hyperplasia. His description of the rachitic symptoms in adults fits well the single case (acute osteomalacia?) tabulated by us; it also fits several additional cases which we observed without obtaining weights of the parathyroids. Hughes, Payne and Latshaw (1925) showed that either sunshine, ultra-violet radiation or the feeding of cod-liver oil prevented the appearance of leg weakness (rickets) in young fowl.

Witschi (1940) has briefly noted, without giving data or providing comment, that he had observed cases of melanism in the weaver finch associated with "a peculiar

type of parathyroid hyperplasia (unpublished)." The finches were caged in the laboratory and presumably received little direct sunlight and no viamin D supplement in the ration. The older literature on melanism in caged wild birds (Beebe, 1907; Rensch, 1925) is not explicit as to exposure to sunlight but it may be assumed that the birds described had received little or no direct sunlight, especially in winter. The parathyroids are not mentioned in these older studies. Beebe (1907) attributed melanistic changes in caged Inca doves (*Scardafella inca*) and finches to humid environment, and apparently extended that explanation to the several cases of melanism in caged birds which he found in the literature. It now seems more probable that the cases observed by Beebe, like our own cases, involved parathyroid disturbance and deficiency of vitamin D.

No comparable melanism has been reported in poultry despite the fact that most observations on vitamin-D deficiency and parathyroid hypertrophy have been made on fowl. This may be due largely to the use of genetically white varieties for these studies, but it is also possible that certain types or shades of color do not become melanistic under vitamin-D deficiency. On this point we note the remarkable fact that the blond ring doves of this colony have shown no clear case of melanism although some thousands of this species have been observed to or beyond the third year of life. These doves were offered the same diet as the *Zenaida* hybrid (above), but a diet that was different from that of the pigeons. The diet of doves contained hemp seed, Kafir or milo, wheat, cracked corn, canary seed and millet.

Rachitic squabs never have shown melanism even when their parathyroids were very large. A more prolonged deficiency, or an element of aging, therefore seems to be necessary for the appearance of melanistic feathers. Something more than chance is also probably responsible for the fact that this type of melanism has not been observed in a male pigeon. On this point it is notable that,

unlike the adult female, the male's supply of calcium and vitamin D is not subject to the special drains and losses which necessarily accompany egg production.

Summary

Five cases of non-genetic partial melanism were observed in adult female domestic pigeons. One similar case was observed in an old male hybrid (*Zenaida* × *Zenaidura*) dove after it became unable to fly.

Two physiological conditions, slight exposure to sunlight and enlargement of the parathyroids, were known to be associated with all of these six cases of melanism. It is considered probable that these conditions were also responsible for previously reported instances of melanism in caged wild birds. In two instances plucked melanistic feathers were replaced by normal feathers following the administration of a concentrate of cod-liver oil (vitamin D).

Parathyroid enlargement is shown to occur regularly in young pigeons reared on a mixed grain diet in the absence of direct sunlight (vitamin-D deficiency). Grossly defective ossification of the bones (rickets) of many such pigeons is reported.

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REVIEWS AND COMMENTS

EDITED BY PROFESSOR CARL L. HUBBS

IN these reviews and notices of current biological publications emphasis is given to books and major articles which fall within the special scope of THE AMERICAN NATURALIST, in that they deal with the factors of organic evolution. REVIEWS AND COMMENTS are meant to include also such general discussions, reports, news items and announcements as may be of wide interest to students of evolution. Except as indicated, all items are prepared by Dr. Carl L. Hubbs, Scripps Institution of Oceanography, University of California, La Jolla, California. All opinions are those of the reviewer.

Configurations of Culture Growth. By A. L. KROEBER, Berkeley: University of California Press, 1944: i–x, 1–882, 8 charts and 1 map. $7.50.

THE amount of historical research that Kroeber expended in this study was matched only by the breadth of his competence. The result is an outstandingly scholarly contribution to the analysis of patterns in the evolution of human culture, as this has been expressed throughout the world in philosophy, science, philology, sculpture, painting, drama, literature, music and the growth of nations. The emphasis is on the configurations of culture in time, in space and in degree of development, rather than on the content, quality and causes of different cultures. The point of view is that of an eminent anthropologist, definitely not that of a biologist. Almost no credence is given to any genetic basis for the differences with time in the degree of cultural development. Genetic changes within human groups having one culture are not categorically denied, but are interpreted as having been of little significance in the growth of cultures. Potential eminence of individuals is regarded as relatively invariable with time, as perhaps also with race. Genius, which is adopted as the index of cultural development in any intellectual field, is held to be suppressed more often than it is realized. The suppression and the realization are attributed primarily to environmental factors.

In his non-biological approach, which will prove disappointing to some, the author seldom presents his conclusions in terms of evolutionary principles. In fact he

seems to avoid even the term cultural evolution, writing, instead, "the configurations of cultural growth." On reading even extracts from the large volume, however, there will occur to a modern evolutionary biologist many correspondences—analogies if you wish—between the generalizations which Kroeber reaches and the concepts of speciation and phylogeny. The more one considers such common principles the more may he become impressed how much there is in common between the laws that regulate the different sorts or levels of evolution.

That potential genius and the cultural developments which might have resulted from pre-eminent minds are ordinarily unrealized through environmental suppression is an assumption which strikingly agrees with a modern evolutionary concept. According to this concept evolution is ordinarily retarded by reason of biotic saturation, and becomes rapid or even explosive when the environment is unsaturated. The idea that geniuses tend to occur more or less contemporaneously, so as to produce peaks of culture, corresponds to the evidence that organic evolution operates by spurts, conditioned by the decline of groups previously dominant or by the availability of new environments. That like cultures evolve repeatedly from the same or similar cultures reminds one of the parallel evolution which results when the evolutionary stage is set—for instance, the repeated origin of viviparity in the cyprinodont fishes, which swim together at the surface in waters that often become so deficient in dissolved oxygen as to endanger the developmentary stages. That like cultures also arise in response to similar conditions may be looked on as an expression of the general principle of convergent evolution. That cultures may persist for long periods in a retarded condition parallels the idea of suppressed evolution. That cultures tend toward bizarre modifications following the peak of their development and preceding the period of decadence reminds one of evolutionary "overspecializations." Cultures as well as groups of organisms may become extinct

either through replacement or through hybridization. Cultures as well as groups generally diffuse from a center of origin. As an inexact and unreliable approximation, the area occupied by either a culture or a group is positively correlated with the age of this culture or group. Environment is a factor of profound importance in both cultural and organic evolution.

In several respects present-day culture is allocated in the decadent stage. This judgment will no doubt be challenged by some. And at this moment one can only wonder what may be the "configurations of culture growth" during the Age of Atomic Energy.

NOTICES OF NEW BOOKS AND ARTICLES

The Influence of Types of Soil upon the Local Distribution of Some Mammals in Southwestern Utah. By ROSS HARDY. Ecological Monographs, 15, 1945: 71–108, figs. 1–19.—Soil texture is shown in this thorough study to be a significant factor directly influencing the local distribution of small burrowing mammals in an arid region. Concentration of soil chemicals and soil moisture act chiefly through the effect of these factors on the vegetation. Other conditions involved in determining the presence or absence of certain types of mammals are the depth and the slope of the soil. The color of the soil affects the distribution of light and dark races.

In agreement with the conclusions by Dice and other workers soil color is indicated as a speciational factor of importance. Where soils of a certain color occur with consistency over fairly large areas, the mammals inhabiting these areas tend to approach the soils in depth of pigmentation and in quality of color. Such speciation in the region studied by Hardy seems to have been accentuated by the presence of an effective distribution barrier, the Beaverdam Mountains, lying between areas where the soils are predominantly different in color.

Weeds of Lawn and Garden. A Handbook for Eastern Temperate North America. By JOHN M. FOGG, JR. Philadelphia: University of Pennsylvania Press, 1945: i–vii, 1–215, 175 figs. $2.50.—This pocket size handbook by the University of Pennsylvania's able botanist, Professor John M. Fogg, Jr., should be of

real value to the gardeners in the section of the country east of the Mississippi River. In a brief but informative introduction the author discusses the general characteristics of weedy species, the geographic origin of weeds, the extermination of weeds, chemical control of weeds and weed ecology. The illustrations are excellent. Amateur gardeners should have no difficulty in identifying a particular plant either in the juvenile or mature stages. There is a glossary, a good index and a bibliography. One wonders why the comprehensive text, "Weed Control," by Robbins, Crafts and Raynor, has been omitted from the bibliography.—THOMAS W. WHITAKER, *U. S. Department of Agriculture, Box 150, La Jolla, Calif.*

Green Cargoes. The Story of the Transportation of Seeds and Plants from Their Original Homes to the Four Corners of the Earth. By ANNE DORRANCE. Garden City, New York: Doubleday Doran & Co., Inc., 1945: 1–187. $2.50.—This book represents an attempt to recount in popular style the history of plant introduction both ancient and modern. In her interpretation of the results of recent research the author appears to have been unnecessarily dogmatic. Mangelsdorf and Reeves would be the last to claim that they had found the complete answer to the origin of corn. At times there is an uncertain mixture of fact and fiction. For example, corn investigators will be surprised to learn that wind blew the seed of maize southward to the Andes and northward to Mexico. There is a limited bibliography. The book might be of interest to gardeners and horticulturists.—THOMAS W. WHITAKER, *U. S. Department of Agriculture, Box 150, La Jolla, Calif.*

Plant Geography and Culture History in the American Southwest. By GEORGE F. CARTER. New York: Viking Fund Publications in Anthropology, 5, 1945: 1–140, figs. 1–27. $1.50. —This monograph attempts to correlate the domestication and subsequent distribution of the important crop plants of the Southwest with the archeological history of this region. On the basis of an extensive ethnological survey, involving two seasons of field work, and a minute sifting of pertinent botanical and archeological literature, the author has built up a credible picture of the interrelations of domesticated plants and cultural history. Although this is probably not the first time

that a union of the two disciplines, botany and archeology, has been used to unravel cultural history, it seems to be the first time the method has been employed so extensively. Admittedly some of the conclusions are tentative, and must await further investigation to establish their validity. However, the author deserves credit for exploring a field that promises to make a worthwhile contribution to both botany and archeology. Plant scientists interested in the domestication of crop plants will find much of value in the sections on cucurbits, maize, tepary bean, kidney bean, and cotton. There is a bibliography of 167 titles, but no index.—THOMAS W. WHITAKER, *U. S. Department of Agriculture, Box 150, La Jolla, Calif.*

The Galapagos Finches (Geospizinae), A Study in Variation. By DAVID LACK. San Francisco: Occ. Pap. Calif. Acad. Sci., 21, 1945: i–vii, 1–159, pls. 1–4, figs. 1–26, 1 map. $2.50.—The Galapagos finches challenge the student of speciation and evolution by reason of the complexity of their variations and the difficulty of ascertaining the structural and physiologic boundaries between species. For Darwin the group posed major problems, but his study of it did not yield an adequate explanation of the origin of its various units; natural selection was too dominant in his thinking. It is only through the application of the "Sewall Wright effect" and of recent advances in knowledge of colonization phenomena in insular birds that Lack has reconstructed a balanced picture of origin which seems to be thoroughly satisfactory.

Hindrances to proper understanding of the group by early workers were inadequate series of specimens and erroneous locality data. Swarth's (1931) detailed taxonomic and nomenclatural treatment largely cleared up the tangle of evidence. David Lack has reviewed essentially the same assemblage of specimens and has proposed some changes in Swarth's taxonomy, but none of these is fundamental. Statistical analysis made by Lack has led to a more conservative attitude in recognizing some weak subspecies; and, in keeping with current trends in ornithology, some closely related geographic representatives have been combined in one species.

The weakest phase of Lack's work is that on sexual dimorphism of plumage and the complicated plumage succession in the age groups within a species. Had the author early possessed a full

realization of the intricacies of molt and plumage sequence when reviewing specimens, better data could have been assembled on these topics. For example, one suspects that there has been some confusion of postjuvenal and juvenal plumages, and the reader can not always be sure that the mixed black plumages referred to are static situations at the time the birds were taken or are the result of molt then in progress. These uncertainties have probably not yielded any wrong conclusions but have merely prohibited the formulation of a clear account of progressive attainment of adult male plumage in the individual and the details of evolutionary regression of sexually dimorphic color. In any event, plumage and molt sequence would doubtless have remained imperfectly known pending further field and aviary study.

Important in Lack's analysis of these finches is his personal experience with them in the field where courtship behavior, interspecific contacts and habitat were observed. Breeding habits of the species are essentially the same. In aggressive and courtship behavior the species appear to recognize each other primarily by difference in size and proportions of the bill. It is this structure also which the taxonomist relies on most in separating them. Closely related species occupy extremely similar or possibly identical habitats and they usually eat the same food. The main genera, however, have different feeding habits and show adaptive radiation.

A unified population of any one species of geospizine is not abnormally variable, contrary to prevailing notions held on this subject. Biologically distinct species may be but slightly differentiated in structure, often less so than mainland species. The complexity of the group lies in the extensive local geographic variation of differing magnitudes. Island populations of each species or even race are often slightly different in mensural characters to a degree insufficient to justify subspecific recognition. The dividing point in bill size between two non-interbreeding, closely related species may have different absolute values on different islands.

Birds have not reached the Galapagos Islands *via* a land bridge, although the islands have been variously connected with each other in the past. The small, isolated islands of the archipelago have fewer species of geospizines and a higher proportion of endemic forms than have the larger or the central islands.

"The most important factors in the evolution of the Geospizinae have probably been the almost complete absence of food competitors and predators and the existence of several islands which provide partial, but not complete, isolation for island forms." Differences between island forms of the same species are considered non-adaptive and due primarily to the random fixation of variability; colonization by an atypical example may be a subsidiary factor.

"Species probably originated mainly through geographically isolated races which later met and kept distinct, but some forms may be of hybrid origin." Characters of closely related species, like those of subspecies, are non-adaptive except that bill characters serve in species recognition. "The species of Geospizinae . . . do not show the degree of overlapping and hybridization sometimes claimed for them, and there is no need to assume for them some quite exceptional method of evolution."

This valuable and sound interpretation of a classic case of variation is a credit not only to the author but to the sponsoring agencies and to the editors who, because of the war, have had much to do with the preparation of the report. The instructive value of the Galapagos finches has by no means been exhausted, but the subject has been nicely brought up-to-date by this work.—ALDEN H. MILLER, *Museum of Vertebrate Zoology, University of California, Berkeley 4, Calif.*

Social Darwinism in American Thought 1860–1915. By RICHARD HOFSTADTER. The American Historical Association. Philadelphia: University of Pennsylvania Press, 1944: i–viii, 1–191. $2.50.—In turning to this book an evolutionary biologist is apt to be disappointed in not finding an adequate consideration of comparative sociology. In condemning a biological viewpoint one might expect a naturalistic approach, which, however, is hardly evident. No impact on the author appears to have been made by the conclusions of Ritter and of some other biologists who have held that cooperation is a major factor in the evolution of biotic societies and in the phylogeny of organisms which have their own social organization or which maintain mutual-aid relations with other organisms. Instead of relying on such views (as he might have done) Hofstadter disavows the Darwinian basis of human societal relations.

There was nothing in Darwinism that inevitably made it an apology for competition by force . . . American society saw its own image in the tooth-

and-claw version of natural selection . . . its dominant groups were thus able to dramatize this vision of competition as a thing good in itself. Ruthless business rivalry and unprincipled politics seemed to be justified by the survival philosophy. . . . This version of Darwinism depended for its continuance upon a general acceptance of unrestrained competition. . . . In time the American middle class shrank from the principle it had glorified, turned in flight from the hideous image of rampant competitive brutality. . . . While Darwinian individualism declined, Darwinian collectivism of the nationalist or racist variety was just beginning to take hold. Darwinism was being made to fit the mold of international conflict-ideologies. . . . The survival of the fittest had once been used chiefly to support business competition at home; now was used to support expansion abroad. These dogmas were employed with success until the outbreak of the first World War. Then, ironically, the "Anglo-Saxon" peoples were swept by a revulsion from international violence. . . . A resurgence of social Darwinism, either in its individualist or imperialist use, is always a possibility as long as there is a strong element of predacity in society. . . . Whatever the course of social philosophy in the future, however, a few conclusions are now accepted by most humanists: that such biological ideas as "the survival of the fittest," whatever their doubtful value in natural science, are utterly useless in attempting to understand society [and so on].

It should be remembered, however, that the qualities that lead to survival in societies and in social organisms may involve cooperation and mutual aid, as well as struggles unto the death.

The Marine Annelids of North Carolina. By OLGA HARTMAN. Duke Univ. Mar. Sta., Bull., 2, 1945: 1–54, pls. 1–10, charts 1–2. $1.00.—Zoologists who may think that the time for faunal surveys by competent specialists is past would do well to peruse this treatise on the annelids of the Beaufort region. The number of species known from the region is about doubled. Two new genera and six new forms are described, and numerous other systematic refinements made. A variety of interesting ecological associations and habitat niches are confirmed or discovered, and are conveniently listed. Other natural history data, as characteristic macroscopic egg masses and characteristic trails or surface marks or tubes, are likewise epitomized. The annelid fauna of the Beaufort area is regarded as relatively rich, due to a mixture of boreal and tropical types. Such studies open the way for research in many biological fields.

SHORTER ARTICLES AND DISCUSSION

GEOGRAPHICAL REGULARITY IN THE VARIATION AND SUPPOSED MIMICRY OF A BUTTERFLY, *LIMENITIS BREDOWII*

THE geographical variation in the butterfly *Limenitis bredowii* has recently been studied by Carpenter and Hobby (1944). This is a North American species very closely related to the tropical American genus *Adelpha*. Forms of the latter are distributed generally in the American tropics and in some places extend slightly beyond the tropics of Cancer and Capricorn. *L. bredowii* occurs from Gutemala through the Mexican plateau to coastal Oregon, Utah and Colorado. Other species of *Limenitis* (or of *Basilarchia*, as the group is better known) are to be found over the whole of North America from the Mexican plateau to southern Canada. It is a matter of individual opinion which generic name should be used for *bredowii*. Sometimes a separate genus, *Heterochroa*, is adopted for this species alone.

Butterflies of these genera are characterized by a basic wing pattern usually consisting of a black ground color broken by white, bluish or orange-brown spots or bands. The relative position of these spots and bands is always the same in the various species; they differ, however, in the size, shape and intensity of color in the light areas.

Limenitis bredowii has been divided into four geographical subspecies inhabiting an equal number of north to south regions. namely, *californica* along the Pacific Coast north of Mexico, *eulalia* in northern Mexico and the adjacent mountain states in the United States, *bredowii* in southern Mexico north of the Isthmus of Tehuantepec and *guatemalensis* in the Guatemala highlands.

Carpenter and Hobby have obtained statistics on the varying size and color characteristics in an attempt at illustrating graphically the convergence of the pattern of this species toward that of the tropical species of *Adelpha* in the region of supposed contact with it in Guatemala. *L. bredowii guatemalensis* is more like some species of *Adelpha* than is the subspecies *californica*, which does not come in contact with *Adelpha*. The implication made by Poulton in 1908 and Carpenter and Hobby now is that of the existence of mimicry between these two groups in the zone of

distributional overlap. It is only fair to state that the authors recognize that a convergence in pattern alone does not prove mimicry.

An explanation alternative to mimicry is that the convergence of *Limenitis bredowii* toward *Adelpha* is related to the physical factors of the environment; such parallel ecogenotypical color variations are shown by many animals. The convergence toward *Adelpha* then would be caused by the action of similar environmental agencies on all the butterflies and mimicry need not be postulated.

The geographical trends of variation in the color pattern may be summarized from the data of Carpenter and Hobby for thirteen characters (Table 1). Ten of these thirteen characters are

TABLE 1

Character number used by Carpenter and Hobby or description	North ..... South			
	californica	*eulalia*	*bredowii*	*guatemalensis*
Color of forewing band	1	2	2	2
4	2	2	1	3
5	1	2	3	3
7	1	2	3	3
8	1	2	3	2
9	1	2	1	3
10	2	1	3	3
12	1	2	2	3
13	1	2	2	2
14	1	2	2	2
Sum of ten characters	12	19	22	26
Shape of hind wing band	1	2	3	3
11	1	1	2	2
15	1	1	3	2

related to a general lightening or darkening of the color of parts of the wings. That is, where the width of a white band is wider in one species than the others, that subspecies has a lighter appearance than the others. The index number (1) has been given to the one of the four subspecies which presents the darkest manifestation, the number (2) the next darkest, etc. Where two or more subspecies are not different in the manifestation of a character, they are given the same number. The four subspecies are arranged in order from north to south. By taking the sum of the numbers thus obtained for each subspecies or geographical area, it is possible to get an index of the degree of its darkness or lightness in color. From north to south, it is clear that such a definite relation does exist. Out of a possible minimum of ten points for darkness, the northern subspecies *californica* has 12.

Out of a possible maximum of 27 points for lightness the southern subspecies *guatemalensis* has 26. The other subspecies enter into the gradient as expected.

The other three characters have no obvious connection with darkness or lightness. It is possible that they are physiologically linked with the climatic change in the same way, but the data do not justify general conclusions.

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A NOTE ON LATERAL PIECE REGENERATION IN *PLANARIA GONOCEPHALA*

RECENTLY, Rulon (1940) has given us a brief review of the subject of experimental control of regeneration in *Planaria* in which it is shown that the work of Child and his associates was concerned with control of correlative factors present in the regenerate, as well as control of regeneration, through the use of various external agents. The fact that a planarian fragment can, under favorable conditions, reorganize itself into a symmetrical and normally proportioned entire worm is well known, but in the course of reconstitution, the regenerating worms often exhibit a certain degree of temporary morphological asymmetry and disproportion. Despite the extensive literature on *Planaria* regeneration, the spatial and temporal relations of symmetry regulation and of the establishment of normal proportionality, and the factors controlling these processes have, so far as we know, been largely ignored. With a view to obtaining information on these points, a careful analysis of lateral piece regeneration in *Planaria gonocephala* is now being undertaken. Experiments already performed show that there is a difference in the rate of symmetry regulation for lateral pieces taken from different physiological levels; sometimes this difference is confined to difference in morphological characteristics. We have also noted what appears to be a regular spatial relationship between the mode of reconstitution and some invisible ground pattern of the sectioned mother worm. It is the purpose

of this preliminary note to give an account of some of these observations.

Experimental Data

A mature worm which had been starved for a week was cut into twelve pieces in the manner shown in Fig. 1. The pieces

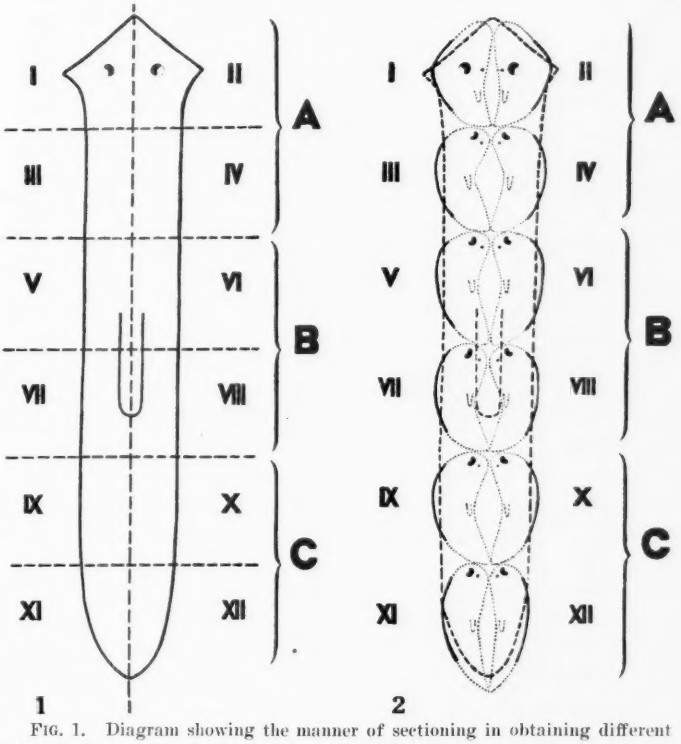

Fig. 1. Diagram showing the manner of sectioning in obtaining different lateral pieces (I to XII) used in this investigation. Letters A, B and C denote the prepharyngeal, pharyngeal and postpharyngeal region, respectively.

Fig. 2. Diagram showing the general relationship between the reconstituted worms and the original animal. The asymmetric configuration with respect to body curvature, eye condition and pharynx position is discussed in the text. Notations have the same meaning as indicated in Fig. 1.

were numbered I, II, III to XII, respectively. They were cultured separately, but a group of ten corresponding pieces taken from ten different mother worms was placed in a single dish,

so as to keep them under identical external conditions, in order to make the results comparable.

The original body axis of each lateral piece could be easily recognized during reconstitution by the different pigmentation of dorsal and ventral surfaces and by the difference between the original intact lateral body wall and the newly healed one. Using these characters as landmarks, it was found that the antero-posterior axis of any reconstituted new worm coincides with that of the mother worm (Fig. 2). This agrees fairly well with the results of experiments made by Bever and Child (1930).

Three clear-cut characteristics: Body shape; number, size and location of eyes; and position of pharynx were chosen for the analysis of symmetry regulation, and changes in these during reconstitution were followed. Transient asymmetry with respect to these characteristics was common to all pieces, quite irrespective of the level of the mother worm from which they were derived. In a total of some 200 reconstituted worms examined during the early period of reconstitution, not a single one showed any symmetric character. At a later stage, however, each lateral piece regulates to form a symmetric and well-proportioned worm.

As regeneration proceeded, the antero-posterior body-axis of a regenerate elongated along a direction inclined always towards the median cut surface, so that in moving the fragment pursued a curving path. In a pair of lateral pieces from any given level, the peculiar body shape of one was the mirror image of that of the other (Fig. 2). The data collected suggest that the relative rate of symmetry regulation for body shape is more rapid than for other characteristics. Thus, at a certain stage of reconstitution, a regenerate may have normal body shape while its eye condition and pharynx position still remain asymmetrical. As regards the level difference, those pieces taken from the post-pharnygeal region of the mother worm appeared to be able to regulate their body shape rather more rapidly than prepharyngeal and pharyngeal fragments, although this difference was not marked.

The regulation of eye symmetry generally took place in two successive stages. Starting with a single eye, the worm formed a pair of eyes dissimilar in size; later these became equal and symmetrically distributed. Without exception, the first eye was the larger member of an asymmetric pair and was located away from the median cut surface, while the smaller one was adjacent

to this surface. Such regular spatial relations in eye regulation may possibly be linked to some invisible structural differentiation of the ground pattern of the mother worm in the medio-lateral direction. When the paired lateral pieces from a given level were each furnished with an asymmetric pair of eyes, their dispositions in the two fragments were mirror images of each other (Fig. 2). As has already been stated, the regulation of eye symmetry proceeded more slowly than that of symmetry of body form. Postpharyngeal pieces were found to possess higher regulative ability for eye symmetry than prepharyngeal and pharyngeal pieces, the difference being more pronounced than that for body shape regulation. At a stage at which postpharyngeal pieces were furnished with a symmetric and well-proportioned eye pair, prepharyngeal and pharyngeal pieces had only a single eye or an asymmetric pair. This is perhaps the most interesting result of our experiments.

The newly reconstituted pharnyx always occupied a position adjacent to the median cut surface as shown in Fig. 2. It was observed that those pieces derived from pre- and postpharyngeal regions reorganized more rapidly into worms with the pharynx symmetrically placed than did pieces from the pharyngeal region. The result indicates that the pharynx of the mother worm may exert some influence on the regulation rate of pharynx symmetry of the pharyngeal pieces.

From these observations it may be concluded that every lateral piece tends to reorganize itself into a worm indistinguishable from the normal individual in every respect except that of size, and that the antero-posterior axis of such a reconstituted *Planaria* coincides with that of the sectioned worm. The fact, however, that the regulatory process in each lateral piece is always preceded by a temporary asymmetry of certain structural characteristics is of some interest. The position may be summarized as follows: First, inclination of body curvature, asymmetric location of the reconstituted pharynx and the position of the small-sized eye are constant features in all regenerates irrespective of their original physiological level. Secondly, the asymmetric configuration of one member of a pair of lateral pieces from a given level is always a mirror image of that of the other. Thirdly, there is a certain difference in the relative rates of regulation of symmetry both with respect to pieces derived from

different levels and with respect to different mutual characteristics. Experimental analysis is being continued.

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ON THE INVERSE RELATION BETWEEN INHERENT AND ACQUIRED PROPERTIES OF ORGANISMS

IN studying the differences between various races belonging to the same species or between similar species of the same genus, it can be recorded that the stronger are their inherent properties in some specific respect, the less they are capable of strengthening these properties under the effect of environmental factors. The existence of inverse relation between the inherent and acquired properties of organisms can be brought into relation with the general property of living systems known as compensation. Geoffroy St. Hilaire realized that with the increase of some organs the others decrease. Rensch[1] mentioned recently several such examples. In these cases the compensation is due to a redistribution of the limited amount of matter in a biological system. It is highly remarkable, therefore, that there exist compensatory relations between acquired and inherent properties in such biological systems as a species or a genus.

Fig. 1 shows the relation between the inherent resistance to salinity and that acquired in the process of acclimatization, in various races of infusoria *Paramecium caudatum*.[2] The acquired resistance is distinctly inversely proportionate to inherent resistance, (Acquired) $= 1 - \alpha$ (Inherent). The coefficient of inverse proportionality (α) in this case is equal to unity. This case can be considered as an example of the complete compensation: the deficiency of inherent resistance is compensated by the acquired resistance in such a way that the total of these two

[1] *Biol. Rev.*, 14: 180, 1939.

[2] G. F. Gause, *Quart. Rev. Biol.* (in press).

properties is maintained approximately the same within the limits of the species. But it is also often observed[3] that $\alpha > 1$ (in the rapid acclimatization of paramecia to increased salinity $\alpha = 3.6$ and to quinine solutions $\alpha = 2.2$). These cases can be considered

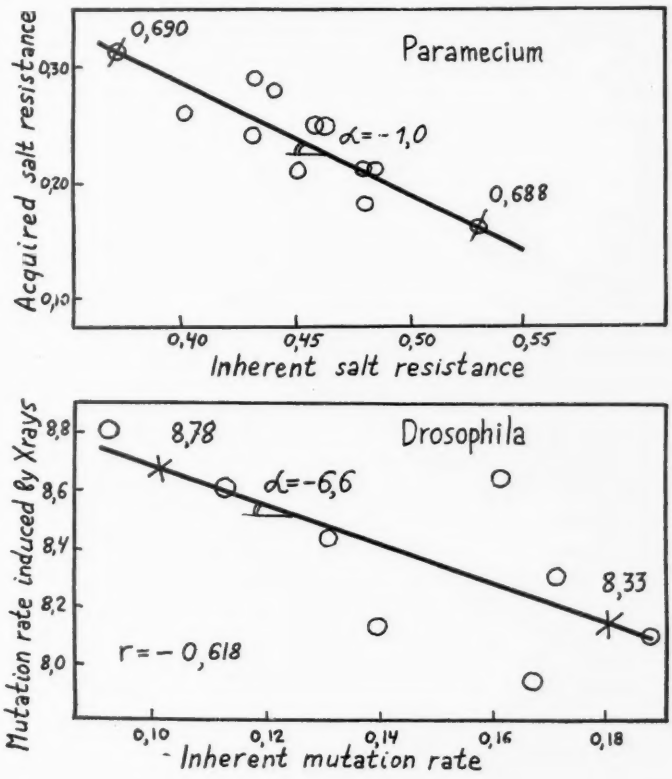

FIG. 1

as the incomplete inverse proportionality between inherent and acquired properties or, in other words, as a non-proportionate compensation. The inherently weaker races evidently overcompensate their weakness, and in respect of the total resistance they exceed inherently stronger ones.

The inverse relation between inherent and acquired resistance to arsenic in different races of infusoria *Colpoda steini* is clearly

[3] G. F. Gause, *loc. cit.*

seen from the figures published by Schuckmann,[4] although the author himself did not notice this regularity.

It is very interesting to refer to inverse relation between inherent mutation-rate and that induced by x-rays in various races of *Drosophila melanogaster*. Timofeeff-Ressovsky[5] concluded that these characters are not correlated with each other. When, however, we plotted his own figures on a graph (Fig. 1), the inverse relation between both variables was easily seen. The coefficient of correlation between the inherent and acquired mutation rates, $r = -0.618$, and having six degrees of freedom we can with the certainty of 90 chances out of 100 accept the existence of this inverse relation. The coefficient α calculated by the method of least squares equals to -6.6. As far as in the light of the data published by Demerec[6] the observations of Timofeeff-Ressovsky are not entirely comparable because of being made over a period of several years, it would be desirable if they were repeated by geneticists in the special experiments designed for that purpose. If confirmed, the process of mutation could be brought under the general principle of inverse relation between inherent and acquired properties of organisms.

The further example is the inverse relation between the inherent number of erythrocytes in blood of different species of mice belonging to the genus *Apodemus*, and the number of erythrocytes acquired under the effect of decreased barometric pressure.[7] In this system, as in those mentioned earlier, the acquired properties are inversely proportionate to inherent ones.

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[4] *Biol. Zbl.*, 60: 239, 1940.
[5] *Biol. Zbl.*, 60: 267, 1940.
[6] *Genetics*, 22: 469, 1937.
[7] G. F. Gause, *loc. cit.*